Frank Harrington

QUAIN'S ANATOMY.

QUAIN'S

ELEMENTS OF ANATOMY

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GENERAL ANATOMY, OR HISTOLOGY.

General Anatomy, or as it is now more commonly termed Histology, is that branch of Anatomy which treats of the structure of the textures. As has already been explained (see Introduction in Vol. I.), the body of every one of the higher animals is made up of organs adapted for the performance of its several functions, and these organs are themselves composed of various tissues or textures. In order that the structure of any organ or part of the body should be understood, it is necessary to study, both together and separately, the several tissues of which it is composed, in order to ascertain their composition and the manner in which they are combined to constitute the organ or part in question. This is chiefly effected by minute dissociations and thin sections, which are observed with the aid of the microscope, and hence the terms "Minute Anatomy" and "Microscopic Anatomy" are also applied to this branch of the science. It is found that when the body is thus dissected or analyzed by the aid of the microscope, that the number of distinct tissues which are met with is comparatively small, and some of these again, although at first sight to all appearance distinct, yet have so much in common in their structure and origin one with another (forms of transition also being met with between them), that the number becomes still further reduced. The elementary tissues which are generally enumerated are as follows :—

Epithelium or epithelial tissue.
Connective tissue with its varieties, including adipose tissue.
Cartilage and its varieties.
Bone or osseous tissue.
Muscular tissue.
Nervous tissue.

The elements which are met with suspended in the fluids of the body, such as the corpuscles in the blood, are also enumerated amongst the elementary tissues. So that we may add to the above list :—

Blood- and lymph-corpuscles.

Many of the organs are formed wholly of a single one of these elementary tissues, or with a comparatively slight intermixture of others. Thus the muscles are made up almost entirely of muscular tissue, with but a small intermixture of connective tissue, blood-vessels and nerves: and the same is the case with the bones; whilst the cartilages are composed wholly of the tissue of the same name. On the other hand, there are certain organs or parts of the body not in themselves distinguished by the preponderance of any special tissue, but compounded of two or more

in varying proportion, which it is nevertheless convenient to describe along with the elementary tissues, on account of their wide distribution in the body, and their uniformity of structure in different parts. These are :—

Blood-vessels.
Lymphatic vessels.
Lymphatic glands and bodies of like structure.
Serous membranes.
Synovial membranes.
Secreting glands.
Mucous membranes.
Integument.

Every texture taken as a whole was viewed by Bichat (Anatomie générale, 1801) as constituting a peculiar system, presenting throughout its whole extent in the body characters either the same, or modified only so far as its local connections and uses render necessary ; he accordingly used the term " organic systems " to designate the textures taken in this point of view. Of the organic systems above enumerated some are found in nearly every organ ; such is the case with the connective tissue, which serves as a binding material to hold together the other tissues which go to form an organ ; the vessels, which convey fluids for the nutrition of the other textures, and the nerves, which establish a mutual dependence among different organs. These were named by Bichat the "general systems," to distinguish them from others such as the cartilaginous and osseous, which being confined to a limited number or to a particular class of organs, he named " particular systems."

Structural elements.—When any tissue is separated by the aid of the microscope into the simplest parts which possess assignable form, such parts are termed the structural elements of the tissue. In almost every tissue, some at least of these structural elements retain to a certain extent the characters of the elementary corpuscles of which the whole body is originally composed. These structural elements are named the " cells " of the tissue. Others again lose for the most part those characters, and becoming elongated and modified in structure, are termed the fibres of the tissue, whilst in other cases, fibres are formed not from the cells but between them. Except the epithelium, all the tissues have fibres as characteristic structural elements, and some, as the connective tissue, fibres of more than one kind. But structurally and chemically as well as functionally, the fibres of the several tissues differ widely from one another.

Intercellular substance.—In addition to these separable structural elements, many of the tissues are composed of a homogeneous matrix or ground substance, in which the structural elements are imbedded. This matrix may exist in considerable quantity, as in some varieties of connective tissue, or on the other hand it may be almost imperceptible in amount, serving merely as a cementing material to connect together the individual tissue-elements, as in epithelium. From its softness, clearness and homogeneity, this ground substance is often apt to escape observation, but its existence may always be rendered evident in consequence of the property it exhibits of combining with salts of silver, a brown deposit of metallic silver occurring in it on subsequent exposure to the light (v. Recklinghausen).

Since all the animal tissues however diversified they may appear, originate as collections of the elementary corpuscles or cells above spoken of, and since these cells remain, many of them, as constituent elements of the formed tissue, we must first of all consider minutely what it is that constitutes an animal cell, what is its structure, its chemical composition, its physical and vital properties, and how and from what the cells of the animal body are developed.

THE ANIMAL CELL.

A typical animal cell is a corpuscle of microscopic dimensions, the cells of the human body seldom exceeding $\frac{1}{300}$th of an inch in diameter, and many being as small as one-tenth of this, or even less. But whether small or large, every typical cell consists of two distinct parts: of the main substance of the cell, which has received the name of *protoplasm* (fig. 1, *p*), and of a minute vesicular structure, generally placed near the centre of the cell, and termed its *nucleus* (*n*).

Fig. 1.

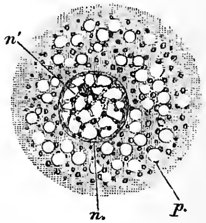

Fig. 1.—Diagram of an animal cell much magnified. (E.A.S.)

p, protoplasm, with vacuoles and granules; *n*, nucleus, with intranuclear network and nucleolus (*n'*).

THE PROTOPLASM OF THE CELL.

The substance to which the term protoplasm has been applied is, in its chemical nature, similar to albumen, being mainly formed of proteid substance. It is characterized by its affinity for certain staining fluids, such as solutions of carmine and hæmatoxylin. Although normally containing a relatively large amount of water combined in its substance, and thereby sharing many of the physical properties of water, it is not miscible with that fluid whilst in the living condition. Protoplasm usually appears to consist of two distinct portions; namely, of a clear, homogeneous semi-fluid material, which is in all probability the essential substance; and of minute granules or particles which are embedded in the hyaline substance, and which by their presence give to the protoplasm a granular appearance. These particles, although in most cells constantly present, are in all probability not essential constituents, but are rather to be regarded in the light of adventitious matter, which has either been formed in the protoplasm itself, or has been taken into it from without. For it is often the case that one part of the substance of a cell is entirely free from granules, whilst other parts may be crowded with them, and it is found, that in such instances the clear non-granular substance is capable of manifesting all the phenomena which are characteristic of protoplasm. Further, when the particles in question are larger and more distinct, it may often be demonstrated that they are different in chemical constitution from the substance in which they are embedded.

In addition to the more solid particles above mentioned, globules of watery fluid are also frequently met with. These refract the light less strongly than the protoplasm itself, and look like clear spaces in it: hence they have been termed *vacuoles*. There may be one, two, or a greater number of such vacuoles in a cell, and in some cases, the protoplasm is filled with them, or occupied by a large space formed by their confluence. This, as is especially evident in vegetable cells, causes the

cell-substance to assume a reticulated aspect. But where vacuoles are accumulated within it to a great extent, it is generally found that the protoplasm no longer exhibits certain characteristic properties, especially that of amœboid movement, presently to be described. Vacuoles are often absent altogether from a cell, and when present, appear and disappear and may become shifted in position from time to time.

What has been above described as the essential part of the protoplasm may itself exhibit a separation into two kinds of substance. For example, in many cells the protoplasm (whether or not granular) may undergo a

Fig. 2.

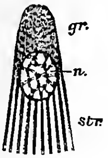

Fig. 2.—Striated epithelium cell, from the duct of a salivary gland; highly magnified. Semidiagrammatic. (E.A.S.).

gr, granular protoplasm ; *str*, striæ ; *n*, nucleus.

differentiation into minute striæ, or fibrils, and clear intermediate substance, and in these cases there is reason to regard the fibrils as perhaps the more important part of the protoplasm. This is the case with the cell-substance in the epithelium cells of many secreting glands or of their ducts (fig. 2, *str*), and with the

Fig. 3.

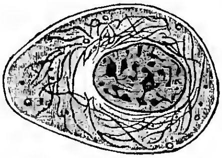

Fig. 4.

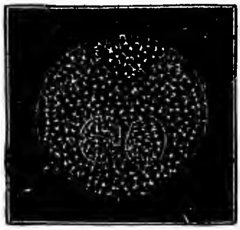

Fig. 3.—A cartilage cell of the salamander, showing fine filaments in the protoplasm (Flemming).

Fig. 4.—Diagram of an animal cell (with two nuclei). (Klein.)

substance of nerve-cells, and Flemming and Schleicher describe the protoplasm of the cells of cartilage as consisting of a homogeneous fluid in which fine particles and minute fibrils are suspended (fig. 3).

This differentiation of the protoplasm in the form of fibrils would appear to be of much more general occurrence than is commonly supposed. According to the observations of Heitzmann, Fromann, Klein, and others, the protoplasmic substance of a cell is to be regarded as composed of a fine network or sponge-work, with a more fluid material in its interstices, the granules which are seen in protoplasm being for the most part the optical sections of some of the fibrils (fig. 4). At the same time it is admitted that true granules may also occur in the interstitial fluid, and in gland cells the products of secretion may here become accumulated. Putting the same idea in somewhat different words, such protoplasm may be described as being highly vacuolated; the substances found in it (granules, materials of secretion) accumulating in its vacuoles.

Protoplasm seems to be weakly alkaline or neutral in reaction, although in some of the lower organisms, blue litmus granules, which had been

taken into the interior of their protoplasm, were observed by Engelmann after a time to become red. This may, however, have been due to a formation of acid around the granules analogous to that which occurs in gastric digestion in the higher animals.

In conjunction with Mr. F. Eckstein, I have made a number of observations upon the white corpuscles of the blood in the same manner, and always found the blue litmus granules which were taken in by the corpuscle to remain unchanged in colour

That the protoplasm of a cell is elastic may be inferred from the manner in which a layer of cells is found to adapt itself to rapid and considerable alterations in the area which it covers; this is the case for instance with the layer of cells which lines the bladder, and with that which covers the outer surface of the lungs.

Contractility of protoplasm.—The most striking and important of the phenomena which are exhibited by cell-protoplasm are those which are due to its possessing the property of contractility. By this is meant the faculty of becoming diminished in diameter in any one direction, and proportionately increased or bulged out in other directions. This property of contractility which protoplasm possesses is shared by, or rather perhaps has become transferred to, other forms of living substance, not generally regarded as purely protoplasmic in nature; namely, vibratile cilia and muscular tissue. But in these the power of diminution is confined to one part or direction only, whereas in unaltered protoplasm the property is possessed by all parts, and is capable of being exerted in any direction. The following are the phenomena exhibited by protoplasm which can be referred to the possession of this property:

1. *Amœboid movement.*—As was first shown by Rosenhof, in 1755, the Proteus animalcule or Amœba, which is composed almost entirely of a mass of protoplasm, exhibits when observed under the microscope

Fig. 5.

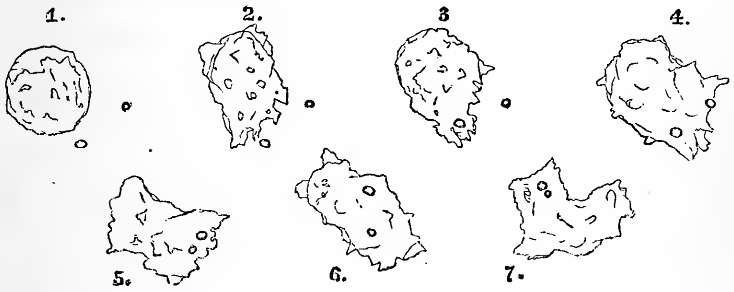

Fig. 5.—Changes of form of a white corpuscle of newt's blood, sketched at intervals of a few minutes. The figures show also the intussusception of two small granules, and the changes of position which these underwent within the corpuscle. (E.A.S.)

the most remarkable spontaneous changes of form; protruding, first on one side then on the other or even at two or more places simultaneously, portions of its protoplasm (pseudopodia), which may be again immediately withdrawn. On the other hand, any one of these projections may remain

protruded, and the substance of the protoplasmic body drawn towards it, so that in this way the amœba is moved about from place to place. Since these and similar changes of form and place of a protoplasmic organism were first distinctly observed and can still be best studied in the amœba, they are aptly termed amœboid. In the higher animals they are most plainly to be seen in the white blood-corpuscle (fig. 5) (where they were first detected by Wharton Jones,) but it is probable that they are exhibited to a slight degree by almost all animal cells in the young state.

2. *Streaming movement of the granules.*—This phenomenon can be seen to occur both in cells which are stationary, and in those which are exhibiting the amœboid movements just described. It consists in the slow motion in definite courses in the protoplasm of the granules which are suspended in that substance. There can be little doubt that the granules are themselves carried along by and swim in the moving protoplasm itself, although in consequence of its homogeneity the currents in it are only indicated by the suspended granules. The currents may not only pass in different directions in the main substance of the protoplasm, but they may also extend along its protrusions, when these exist, and it occasionally happens that there may be present in one and the same protrusion both an outgoing and an incoming stream.

These streaming movements have been longest known in the protoplasm of vegetable cells (Vallisneria, Chara, Tradescantia, &c.), but they are very strikingly manifested in the protoplasmic substance of the lower animal organisms, and there is reason to believe that they occur in many of the fixed cells of the tissues of the higher animals, although here much more difficult of detection. In the white corpuscles of the blood the granules in the protoplasm are seen to stream into the processes, which when first protruded are generally free from granules; but in this case the flow of particles may perhaps be caused in a different way from that in the other instances above given.

3. *Intussusception of foreign particles.*—When any minute foreign particle comes in contact with the protoplasmic substance, the particle is apt to adhere to it. But what is more remarkable, the particle does not remain in contact with the external surface; it becomes on the contrary enwrapped by processes of the protoplasm, and then withdrawn gradually into the interior, where it may remain for some time without change, being moved about by any currents which exist in the cell, and carried along by the changes of place which the cell undergoes (see fig. 5). Eventually such foreign particles may be extruded again. If, on the other hand, the particle is of considerable size as compared with the protoplasm with which it comes in contact, the latter extends around and over it so as to envelope it more or less completely. This phenomenon of intussusception seems thus to be partly dependent upon amœboid movement, and partly upon the production of currents in the protoplasm.

The protoplasm of ordinary vegetable cells being for the most part enclosed in a continuous cell-wall, instead of being naked like that of a typical animal cell, cannot be protruded in the shape of pseudopodia beyond that wall nor does it for the same reason exhibit the phenomenon of intussusception just described. But it is, nevertheless, as before mentioned, capable of active streaming movements, which are influenced by the same conditions (heat, electricity, and the like) as are the movements of animal cells.

Conditions influencing the contractile manifestations of protoplasm.—All these several manifestations of contractility, are influenced in the same manner by similar external conditions. Thus it is found that variations of temperature have a marked effect upon all. In warm-blooded animals the phenomena cease altogether to be exhibited, if the protoplasm which is under observation is cooled to below a temperature of about 10° C, although they will be resumed on warming the preparation again, and this even if it has been cooled to 0° C., or even a little lower. And when warmed gradually, it is found that they become more and more active as the temperature rises, attaining a maximum of activity a few degrees above the natural temperature of the body, although if maintained at an abnormally high temperature, the movements are not long continued. A temperature a little above this maximum, rapidly kills protoplasm, producing a stiffness or coagulation in it (heat-rigor), which is preceded by a general contraction. From the condition of rigor the protoplasm cannot be recovered.

The contractility of protoplasm is dependent upon supply of oxygen. If this be withheld, the movements will it is true proceed for a time as usual, but this is because protoplasm like other forms of contractile substance, such as muscle, has the power of storing away and using oxygen in some form of combination. For it is found that the active manifestations will not proceed indefinitely in the absence of oxygen, but cease after a time, to be renewed only on the accession of fresh oxygen.

Many reagents in solution influence the activity of protoplasm. Some of these act by adding to or subtracting from the water which it contains. As a general rule the imbibition of water by the protoplasm, accelerates its activity up to a certain point varying according to the source of the protoplasm which is under observation (Thoma), but beyond that point addition of water produces a destructive effect. A comparatively slight amount of desiccation, is, so far at least as regards the protoplasm of the higher animals, destructive of vitality, but this statement does not hold good for the protoplasm of many of the lower animal and plant organisms.

Amongst reagents acids, although very weak (even carbonic acid), stop the contractile manifestations, alkalies, on the other hand, if sufficiently dilute, increase at first their activity. They are stopped by chloroform and ether, but may be again resumed on the removal of those vapours. Some poisons (e.g. veratria) rapidly arrest the movements in question.

Effect of electrical and other stimuli upon protoplasm.—The effect of electrical stimulation upon protoplasm which is exhibiting either amœboid or streaming movement is, if sufficiently strong, to cause an immediate cessation of those movements, accompanied by a withdrawal into the main substance of any processes that may have been protruded. If the stimulation be intermitted, the movements will recommence, provided the shock has not been so severe as to injure the living substance.

Abrupt changes of temperature, and mechanical stimulation such as is produced by sudden pressure or harsh contact act in a similar manner.

These effects are probably to be explained by supposing that the stimulation produces a contraction of the substance in every possible direction, for the result is that the cell subjected to stimulation, assumes, if it be capable of doing so, the spherical form. Whether there is any actual diminution in volume accompanied by expression of fluid must remain undetermined.

Of chemical and other changes which occur in the protoplasm of cells.—The protoplasm of a cell may become variously altered in chemical constitution, all such changes tending to diminish the original activity of the cell and to fit it for a special function. An alteration often met within older cells is the conversion of the outer portion of the protoplasm into a comparatively hard layer, which constitutes an investment for the remainder, and in this way approximates the cell more to the vegetable type. Such a transformation is met with in a high degree in the stratified epithelia, in which the cells of the uppermost layers become almost entirely transformed into dense horny scales.

Another change which is apt to occur is the deposition within the cell of various chemical principles, which are either derived directly from the plasma of the blood, in which in such cases they pre-exist, or are elaborated by the cell itself from some other constituent of that fluid. Examples of these changes are to be found in the deposit of fat (fig. 7, *f*) and pigment, and of the peculiar constituents of certain secretions within the cells of the tissue or gland producing them (see fig. 6).

Fig. 6.

Fig. 6.—Crystals of uric acid in cells, from the renal organ of a mollusc. (Boll.)

In the two left-hand figures, the crystals are enclosed in vacuoles.

Sometimes changes of the same kind are connected with the production of new structures in a cell, as in the formation of red blood-corpuscles within the cells of connective tissue (fig. 7, *h*, *h*).

Fig. 7.

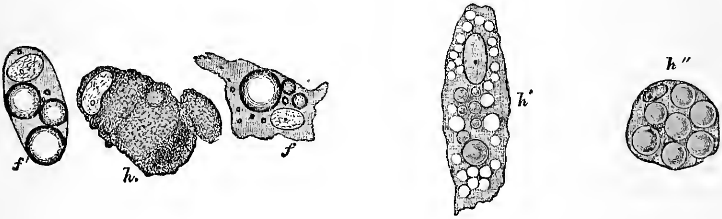

Fig. 7.—Deposit of fat and formation of red blood corpuscles within connective tissue cells. (E.A.S.)

f, *f*, cells in which fat globules are being deposited; *h*, *h*, cells in which red blood corpuscles are becoming formed.

THE NUCLEUS OF THE CELL.

The nucleus (fig. 1, *n*) is a minute vesicular body, placed generally near the centre of the cell and embedded therefore in the protoplasm. In form it is round or oval in most cases, but it may be irregular in shape. Its size relatively to that of the cell varies much in different instances, for sometimes there is so small an amount of protoplasm that the nucleus appears to occupy nearly the whole cell. This is the case for example with many of the cells which are met with in lymphatic glands, and the small nerve-cells which are found in the cerebellum and elsewhere. On the other hand, the protoplasm of the cell, whether altered as in the

superficial layers of stratified epithelium, or unaltered as in many of the white corpuscles of the blood, may much exceed the nucleus in bulk. In absolute size, the nucleus does not exhibit any very considerable variation in different cells of the same animal. There are, however, some notable exceptions; thus the nucleus is absolutely much larger in the ovum or egg-cell and in many nerve-cells than it is in other cells of the body.

Structure of the nucleus.—In the typical resting condition the nucleus is always bounded by a well defined wall, which encloses the nuclear contents. These are of two kinds, formed and amorphous. To the latter the term *nuclear fluid* is sometimes applied, and the former is sometimes named *nucleo-plasm* or *karyo-plasm;* this term being used to include also the substance which forms the wall of the nucleus. But it is by no means certain that the homogeneous amorphous substance which occupies the interstices of the nucleo-plasm is of a fluid nature, so that it might probably be better to term it the *nuclear matrix.* The name nucleo-plasm, on the other hand, although not altogether without objection, is probably as convenient as any other that has been proposed.

The nucleo-plasm often takes the form of one or more strongly refracting granules or globules, which are named *nucleoli.* The nucleoli may be suspended, isolated, in the nuclear matrix, or they may be connected with one another, if they are more than one, and with the nuclear wall by a network of fine filaments, which also form part of the nucleoplasm (fig. 8). There is little doubt that these various parts of the

Fig. 8.

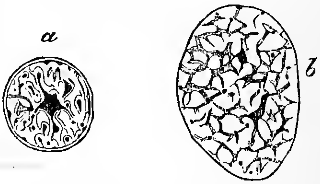

Fig. 8.—Cell-nuclei, exhibiting the reticulate appearance of the nucleo-plasm. (Flemming.)

a, nucleus of liver-cell (carp); *b*, nucleus of a connective tissue cell.

nucleus are capable of undergoing spontaneous changes in relative amount and form. Thus it is found that when treated with hæmatoxylin the nuclear matrix has in some cases a considerable affinity for that colouring matter, in others very much less or none at all; the latter when the nucleoplasmic fibres are much increased in amount, as is the case when the nucleus is about to undergo division. From this it is inferred that a substance readily becoming stained by hæmatoxylin was in the first instance suspended uniformly in the nuclear matrix and has subsequently become shed out, so as to increase the bulk of the already existing nucleoplasmic fibres.

We have also observations showing that spontaneous changes of form may occur in nuclei. Thus both Flemming and Stricker have noticed, in preparations of blood, nuclei, which had been set free by rupture of the corpuscles to which they belonged, exhibiting spontaneous changes of form, and Klein has made a similar observation upon the large nuclei of the glands in the skin of the triton. Within the living epithelium-cells of the tail of salamander larvæ, Flemming also noticed alterations taking place in the outline of the nuclei. Furthermore, several observers have noticed and described spontaneous changes of form in nucleoli, which they have compared to the amœboid movements of protoplasm.

There are still some considerable differences of opinion regarding the structure of the nucleus. Thus, while Flemming looks upon the nucleoli as perfectly distinct from the network of nucleo-plasm which may be present with them, Klein is inclined to regard them as nothing but the optical expression of some of the filaments of the intra-nuclear network which, passing in the direction of the axis of vision, appear as dots instead of fibres, or at least as enlargements merely of the nodes of that network, and composed of the same substance.

Eimer describes a more complicated arrangement as existing in many nuclei in the form of a clear "hyaloid" zone, encircling the nucleolus, and bounded by a circlet of granules, which are united with the nucleolus by fine radial filaments. It is difficult to avoid thinking that the appearances described by Eimer must be mainly an optical effect produced by reflexion of light from the sides of the nucleolus.

Chemical nature of the nucleus.— From the affinity which, in common with protoplasm, it possesses for certain colouring matters, as well as for other reasons, the nucleus has been supposed by some eminent histologists (and notably by Lionel Beale, who has applied the term "germinal matter" to both) to be identical in nature with that substance. Its behaviour, however, with many reagents is altogether different; and in general it may be said that it offers greater resistance to their action than the substance which surrounds it.

Thus dilute acids and digestive fluids, which destroy protoplasm, only render the nucleus more distinct. Moreover, as we have seen, it stains much more intensely with hæmatoxylin and many other reagents, than does protoplasm, and, on the other hand, it remains in some cases unstained by reagents which colour protoplasm intensely, for example, solution of chloride of gold. So that chemically at least there is no doubt a considerable difference between the nucleus and the protoplasm. Still when we regard the spontaneous changes which are manifested by both, and especially the important part which the nucleus plays in the division of the cell, as will be immediately described, there is much in favour of the view which regards the nucleus as a portion of the living substance, which is set aside, altered it is true in chemical nature, to preside over the multiplication and reproduction of the cell; and in favour of this there are observations which show that under certain circumstances, the nucleus may enlarge at the expense of the protoplasm, even to the extent of absorbing the greater part of the latter, so that the whole cell is little else than nucleus; and indeed, this relative increase of size of the nucleus seems to be a change which constantly precedes the phenomena of cell-division.

The observations on the spontaneous movements of the protoplasm of the lower animal organisms by Dujardin, Meyer, Huxley, M. Schultze, J. Müller, Siebold, and others, and of that of the white corpuscles of the blood and other cells by Wharton Jones, Kölliker, Virchow, Kühne, and M. Schultze led eventually, as has been pointed out by Stricker ("Handbook of Histology," p. 2), to a clearer understanding of the nature of cells and its formulation by *E. Brücke* ("Die Elementarorganismen" Wiener Sitzungsb. 1861) and *M. Schultze* ("Ueber Muskelkörperchen und das was man eine Zelle zu nennen habe" Reichert and Du Bois-Reymond's Archiv, 1861); by whom it was demonstrated that the cell membrane, which entered materially into the conception of the structure of the animal cell as understood by its discoverer Schwann, and his immediate successors, is in no way an essential part of it. It should be added, however, that the existence of animal cells destitute of a cell envelope was clearly recognized by Schwann himself ("Microscopische Untersuchungen," 1839, p. 209). The fundamental importance of the protoplasm and nucleus (germinal matter) as distinguished from the cell-membrane and other

products of the protoplasm (formed material) was independently asserted by *Lionel Beale* (" On the Structure of the Simple Tissues of the Human Body," 1861).

MULTIPLICATION OF CELLS.

Cells multiply by division, the process being as a rule binary, each cell dividing into two other cells, these again into two, and so on. The division of a cell is preceded and accompanied by certain changes in the form and constitution of the nucleus; with comparatively unimportant modifications, these changes are similar both in the vegetable and in the animal kingdom. Our knowledge of them was originally due to the researches of Strasburger, made chiefly upon the vegetable cell, but was soon extended to the animal cell by numerous observers, amongst whom may be mentioned in the first instance Eberth, Mayzel, and Flemming. It is the account given by the last-named observer which will be adhered to in the following description of the phenomena which accompany cell-division.

The mode of cell division which is characterised by the changes in the nucleus here to be described is sometimes known as " indirect cell-division," to distinguish it from the division of a cell by simple constriction of its nucleus and protoplasm into two (or more) parts (" direct cell multiplication,") which until recently was thought to be the universal method, although now believed to occur rarely, if at all.

When a cell is about to divide, its nucleus, which may previously have presented the usual structure characteristic of resting cells—consisting, namely, of a vesicle containing a network of nucleoplasmic

Fig. 9.

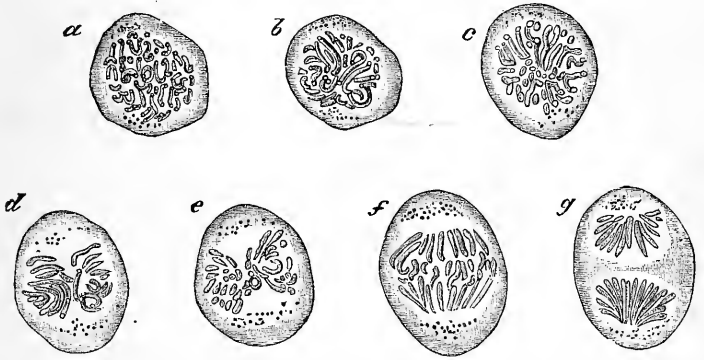

Fig. 9.—Stages in the division of the nucleus of a living epithelium cell in the epidermis of a salamander-larva. (Flemming.)

a, cell showing the nucleus transformed into a mass of contorted filaments (corresponds to *b* and *c* of fig. 10); *b*, the nuclear filaments have become fewer and more united, and begin to assume a converging arrangement (compare *d*, *e*, *f* of next figure); *c*, stellate form (compare *g*, fig. 10); *d*, *e*, hourglass contraction of the nucleus which gradually passes off and the form *c* is resumed. This may occur more than once: eventually the filaments accumulate in a direction parallel to one another near the centre of the cell, and then gradually separate into two sets as shown in *f* (*i*, *j*, *k* in fig. 10). These as they retire towards the poles gradually resume the stellate form *g* (*l*, fig. 10). The time occupied whilst the stages above represented were passed through was about three hours.

fibres which stain darkly with carmine, and a nuclear matrix staining less deeply (fig. 10, *a*)—becomes transformed in the following way. In

the first place it appears rather larger and less defined, and its interior is found to contain a close interlacement or skein of contorted filaments of nucleoplasm (fig. 10, *b*, *c*), to which the nucleoli and intranuclear network have given place, whilst the nuclear matrix has lost its affinity for staining fluids. Meanwhile the body of the cell has become, if

Fig. 10.

Fig. 10.—Epithelium cells of salamander-larva in different stages of division. The cells were hardened in picric or chromic acid, and stained with hæmatoxylin or safranin. Highly magnified. (Flemming.)

a, resting cell, showing parts of the nuclear network which is stained, as is (slightly) the nuclear matrix ; *b*, first stage of division, nucleus transformed into a mass of closely contorted filaments ; *c*, second stage, filaments larger and less closely arranged : in this and all the other figures except *a* the nuclear matrix is clear ; *d* (rather more magnified than the rest), filaments larger and becoming arranged in loops : this is more evident in *e*, where they collectively have a rosette-like appearance enclosing a central clear space ; *f*, filaments converging towards the centre, the nucleus passing into the stellate phase, *g*, in which the peripheral loops of the rosette have become severed ; *h*, longitudinal splitting of the filaments ; *i*, equatorial stage of Flemming ; the nuclear filaments parallel with one another in the centre of the cell ; *j*, commencement of a separation into two sets ; *k*, separation more advanced ; *l*, stellate phase of daughter-nuclei ; *m*, rosette phase of the latter ; *n*, filaments becoming again irregularly contorted ; *o*, *p*, gradual passage of daughter-nuclei into condition of rest (network, *q*). The division of the protoplasm is seen to begin in the stage represented by *m* and to be rapidly completed (at *n*).

previously flattened or elongated, more rounded in form, and it may often be observed that the granules which are present in the protoplasm become arranged into two groups placed on each side of the cell (fig. 9, *a*).

This condition of the nucleus passes gradually into one in which the filaments of nucleoplasm are less fine and also less contorted, whilst they are rather more separated from one another, as if the finer filaments had shortened themselves, and in shortening had become proportionately thicker and further apart (fig. 9, *b* ; fig. 10, *d*).

It is difficult to say if there is really only one filament twisted in a complicated manner on itself, or if there are several intertwining filaments. But whether originally only one or several, in the next stage, if the latter is the case, their ends join so that there is to all appearance only one long nucleoplasmic fibre which becomes arranged in such a manner as to form a rosette-like structure, looping alternately in and out from a central space which is left clear (fig. 10, *e*). Long before this the membrane of the nucleus has disappeared as such, apparently being absorbed into the skein-like system of nucleoplasmic fibres, but a zone of clear substance, perhaps derived from the nuclear matrix, separates that system of fibres from the protoplasm of the cell.

The fibre or fibres next separate into portions of equal length, (the separation generally occurring in the rosette stage, although it may happen earlier). The change often begins at those parts of the rosette which are to become the poles of the nucleus. The peripheral loops of the rosette become broken through, whilst the central loops tend inwards and converge towards the centre of the rosette, so that a star is the result (fig. 9, *c*; fig. 10, *f*, *g*). Occasionally the convergence is towards two points instead of one, so that a double star is produced ; the division of the nucleus being thus early indicated. This astral or amphiastral condition persists for some little time, but not always without alteration, for the aster is sometimes observed to undergo changes of form and size, becoming alternately more flattened, and again more rounded, and this so rhythmically as to have suggested the change being spoken of as the systole and diastole of the star.

The fibres which form the rays of the star often become split longitudinally, the cleavage extending gradually from their free end towards their centre, the result being that they are both more numerous and finer (fig. 10, *g*; *h*).

In the next phase, which is termed by Flemming the equatorial stage of division (fig. 9, *f* ; fig. 10, *i*, *j*), the V-shaped nucleoplasmic fibres have become collected, parallel to one another, in the middle, often leaving a space clear at either end ; these spaces being opposite to the poles of the nucleus. Collectively the fibres form a somewhat barrel-shaped system at this stage : in each fibre the angle of the V is directed towards one of the poles of the nucleus, whilst the limbs either interlace or abut against one another at the equator. Presently the fibres of the system are seen to be separating into two groups (fig. 10, *k*), leaving a clear space in the plane of the equator, and the two groups, gradually become more distinct from one another, travel towards the poles of the nucleus.

From the two groups of fibres thus separated the nuclei of the two new cells become derived, and we may speak of them, therefore, as the nucleoplasmic fibres of the daughter-nuclei. The mode in which they resume the structure of ordinary nuclei is by a reversal of the phases which were exhibited by the mother-nucleus. Thus the nucleo-

plasmic fibres in each of the two daughter-nuclei take on first of all a stellate disposition (fig. 10, *l*), next the rays of the star become united in loops, so that the rosette condition is reproduced (fig. 10, *m*), then each rosette becomes a skein of contorted fibres (fig. 10, *n*, *o*) and finally the normal condition of a resting nucleus is attained with its nuclear membrane, and intranuclear network (fig. 10, *q*)

In addition to the nucleoplasmic fibres, the changes of which have been described above, other fibres may often be seen in the clear substance which occupies the ends of the mother nucleus in the equatorial phase, converging from the equator to the poles; and, when the daughter-nuclei have become separated, bridging across the interval between them (see fig. 11). These fibres do not, like the others, become stained with hæmatoxylin, and are hence termed "achromatic" by Flemming: they are much better marked in some cells than in others, and they probably exercise an important influence as guides, along which the movements of the other fibres take place. In the division of the ovum, and in the multiplication of the nuclei of vegetable cells the achromatic fibres are exceedingly prominent and form a spindle shaped system of a characteristic aspect and looking at first sight very different from those nuclei the division of which has just been

Fig. 11.

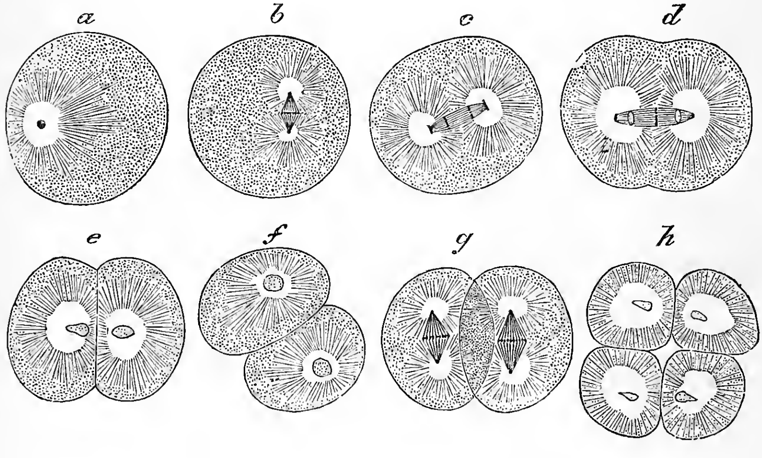

Fig. 11.—Stages in the division of the ovum or egg-cell of a worm. (Strasburger.)

a, resting state; *b*, nucleus transformed into a spindle-shaped system of fibres, which are provided with thickenings at the equator of the spindle; *c*, separation of equatorial thickenings into two parts which gradually travel towards the poles of the spindle and there become transformed into new (daughter) nuclei, whilst the protoplasm at the same time also separates into two parts (*d*, *e*, *f*); *g*, repetition of the division process, formation of spindles in daughter cells; *h*, result of the division of these. (The nuclear filaments shown in fig. 10 are here probably only represented by the thickenings at the equator of the spindle-shaped system, which is mainly formed by fine straight filaments, which stain far less with hæmatoxylin than the others, and on account probably of their less distinctness and want of colouration are not seen in the nuclei represented in fig. 10.)

described. But transitions which are met with indicate that the spindle and its transformations represent merely simplified modifications of the usual type, resulting it may be from the scanty amount of nucleoplasm or substance staining with hæmatoxylin, and the relatively large amount of achromatic material in those nuclei in which the spindle is prominent.

Meanwhile the protoplasm of the cell has begun to collect itself towards each of the two new nuclei. This often commences whilst the daughter-nuclei are yet in the stellate phase. By the time that they have arrived at the rosette stage, the protoplasm has usually divided into two equal halves (fig. 10, *m*), the process being generally accompanied by a constriction which extends in from the exterior, and is presumably effected by the powerful and equal attraction which is exerted upon it by the new nuclei.

In proof of some such influence, may be adduced numerous instances in which the granules of the protoplasm become arranged in lines converging towards the poles of the mother-nucleus, or towards the daughter-nuclei, thus producing an amphi-astral appearance in the cell. This is often very distinct in dividing ova (fig. 11).

The division of the cell is now complete. The two daughter-cells are of course each at first smaller than the mother-cell, but they soon grow, and the process may recommence and be repeated in them, and in this way cell-multiplication may be exceedingly rapid. The cells commonly become entirely separated ; in some tissues, however—cartilage, for instance—they may remain in proximity, producing thus groups of two or four newly-formed cells, which, in the case of that tissue, may at first be enclosed in a common cavity of the matrix : this process of multiplication has been styled "endogenous." But it is in all probability essentially the same as in the less solid tissues.

Fig. 12.

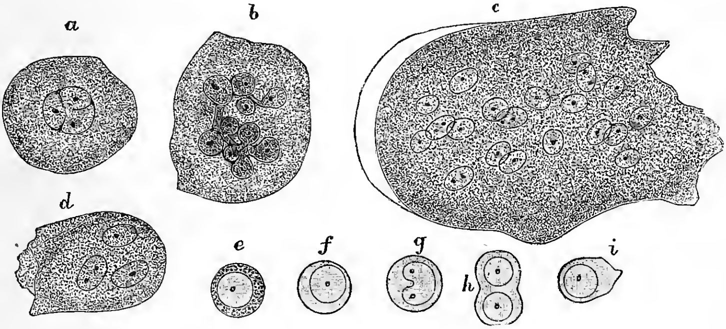

Fig. 12.—Multinucleated cells from the marrow. Highly magnified. (E.A.S.)

a, a large cell the nucleus of which appears to be partly divided into three by constrictions ; *b*, a cell the enlarged nucleus of which shows an appearance of being constricted into a number of smaller nuclei ; *c*, a so-called giant-cell with many nuclei ; *d*, a smaller cell with three nuclei ; *e*—*i*, other cells of the marrow.

Sometimes, a multiplication of nuclei within a cell occurs without immediate separation into new cells, as in the white corpuscles of the blood in which it is common to see two, three or even more nuclei ; in the large multinucleated cells which are found in the medullary cavities of bone, (fig. 12), and in the spermatic cells of the testis, the nuclei of which may undergo division a number of times prior to the separation of a part of the protoplasm around each. The division of the cell itself occurs in these cases by a portion of the protoplasm gathering around

each of the daughter-nuclei, and the original cell thus dividing into as many new cells as there are nuclei in it.

Instances have been observed out of the body in which the amœboid movements of the protoplasm seem to have been concerned in the cell-division, but this occurrence is seldom, and most likely accidental; indeed, it is found, as a general rule, that whilst cell-division is proceeding, the external manifestations of activity of cell-protoplasm cease almost entirely.

The following are the more important phases of change of the dividing nucleus put in tabular form (Flemming)* :—

Mother-nucleus. ↓		*Daughter-nuclei.* ↑
Network.	(State of rest).	Networks.
Skein.		Skeins.
(Rosette).		(Rosettes).
Aster.		Asters.
	Equatorial grouping of fibres. →	

OF THE ORIGIN OF CELLS.

So far as is at present known, every cell in the animal body has been derived from a previously-existing cell. If we trace back the development of the cells of which the body is at one time entirely composed—the so-called *embyronic cells* (fig. 13),—we find that they are originally produced by the division of a single cell derived from the female parent, and termed the *ovum* or *egg-cell*.†

Fig. 13.

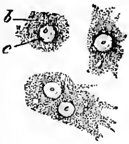

Fig. 13.—Three cells from early embryo of the cat. Highly magnified. (E.A.S.)

b, protoplasm ; *c*, nucleus with nucleolus. The lowermost cell has two nuclei.

Fig. 14.

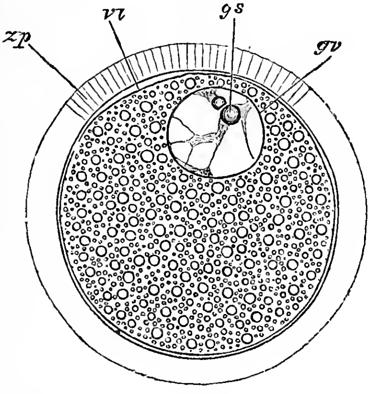

Fig. 14.—Ovum of the cat ; highly magnified. Semi-diagrammatic. (E.A.S.)

zp, zona pellucida ; *vi*, vitellus ; *gv*, germinal vesicle ; *gs*, germinal spot.

Cell-nature of the mammalian ovum.—The ovum (fig. 14), as it occurs in the female organ or ovary, is a large cell enclosed in a distinct envelope ; otherwise consisting like other animal cells of protoplasm and a nucleus.

* The term "karyokinesis" is sometimes applied collectively to the changes of a dividing nucleus.

† In the account which follows of the early changes which the ovum undergoes, leading to the production of the embryonic cells. no attempt is made to give a complete history of the early developmental processes, but the subject is merely alluded to in connexion with the relation which the egg-cell bears to other cells of the animal body. The full description of the processes in question will be found in the chapter on Embryology, at the end of this volume.

Special names have long been applied to these parts in the ovum. Thus the nucleus of the ovum is termed the *germinal vesicle* (*gv*), and the main collection of nucleoplasm within it—the nucleolus—is termed the *germinal spot* (*gs*); while the protoplasm of the cell has been named the *vitellus* or *yolk* (*vi*). Enclosing the whole is a thick radially striated structure, the *zona pellucida* (*zp*).

This egg-cell or germ-cell is not, at least in the higher animals, capable of undergoing complete cell-division, and thus initiating development, without first passing through certain changes which are not, it is believed, shared by ordinary cells. To these changes in the ovum the terms *maturation* and *fertilization* are applied, and their result is the production of the first embryonic cell.

The maturation of the ovum essentially consists in the extrusion of a portion of the nucleus or germinal vesicle, together with a small amount of the protoplasm or vitellus. This process of extrusion appears to be really a division of the cell into two very unequal portions, the larger of the two being still termed the ovum, the smaller, which may again divide into two, being termed a polar globule, or it might be better to term it an extrusion-globule. The following is the way in which this change becomes effected*:—Soon after the ovum leaves the ovary, or immediately before, its nucleus, which previously

Fig. 15.

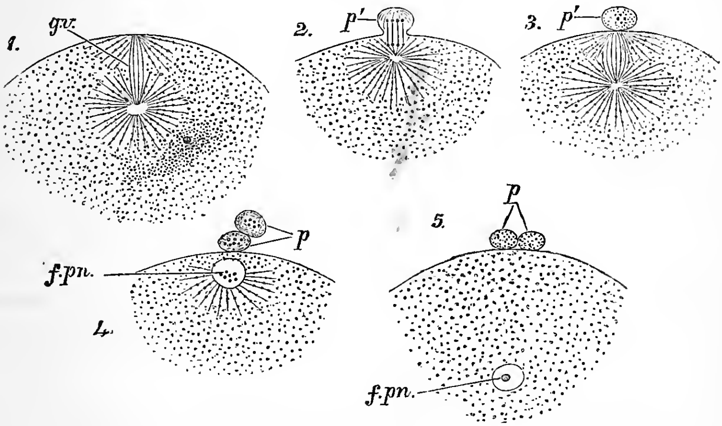

Fig. 15.—Stages in the formation of the polar globules in the ovum of a star-fish (from Hertwig).

g.v, germinal vesicle transformed into a spindle-shaped system of fibres; *p'*, the first polar globule becoming extruded from the surface of the ovum; *p*, *p*, polar globules completely extruded; *f.pn*, female pronucleus.

presented the structure typical of the nucleus of a resting cell, shows indications of a change, and becomes transformed into a spindle-shaped system of fibres which is situated near the surface of the vitellus (fig. 15, *g.v*). Presently one pole of the spindle is protruded from the surface of the vitellus (*p'*) into a space (perivitelline space) between the zona pellucida and the vitellus, caused by a shrinking of the latter. In the next place the substance of the nucleoplasmic fibres gradually collects towards the poles of the spindle in much the same way

* The description which follows applies to the ovum of the star-fish as observed by Fol and Hertwig; but the researches of Ed. van Beneden indicate that similar phenomena attend the extrusion of the polar globules in the mammalian ovum, although on account of the difficulties of the observation all the phases have not as yet been seen.

as during the division of the nucleus in an ordinary cell, and two daughter-nuclei are thus formed, one remaining in the ovum, and the other, together with a very small amount ef the vitellus, becoming free in the perivitelline space as a polar globule (fig. 15, 3, *p'*). This may again undergo division, or a second polar globule may be produced from the nucleus of the ovum in the same way as was the first. The nucleus of the ovum now moves again towards the centre, there to await the advent of the fertilizing agent. Since it is now somewhat different from an ordinary nucleus in its incapability to initiate the division of the cell without the access of a fertilizing agent, as well as in structure, no nucleoplasmic network being visible, it is no longer termed the nucleus, but the *female pro-nucleus* (fig. 15, 4, 5 *f.pn*).

Arrived at the condition above described, the ovum seems incapable of undergoing further change until it has received and blended with a portion of one of the male generative cells. The latter give off, in a manner which will be described when the male organs of generation are treated of, minute portions of their nuclei and protoplasm in the form of the so-called spermatozoa. These consist of an extremely minute particle of nucleoplasm termed the head, a small intermediate mass of protoplasm named the body or neck, and a long spontaneously vibratile filament, the tail, by the movements of which they

Fig. 16.

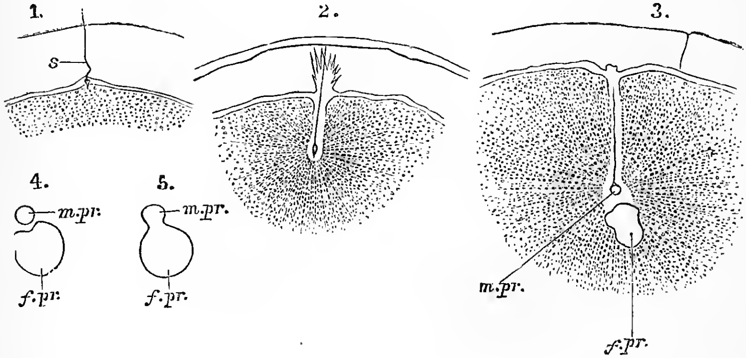

Fig. 16.—Fertilization of the ovum of an echinoderm (Selenka).

s, spermatozoon ; *m.pr*, male pronucleus ; *f.pr*, female pronucleus.

1. Accession of a spermatozoon to the periphery of the vitellus ; 2. Its penetration, and the radial disposition of the vitelline granules ; 3. Transformation of the head of the spermatozoon into the male pronucleus ; 4, 5. Blending of the male and female pronuclei.

are propelled, and thus assisted to reach the ovum. This accomplished, they pierce the zona pellucida, and the head of a spermatozoon, generally of only one, becomes buried in the periphery of the vitellus (fig. 16, 1). The imbedded head enlarges, and becomes transformed into a clear spheroidal body, the *male pro-nucleus*, which, as the lines of vitelline granules which converge towards it indicate, exerts a powerful influence upon the protoplasm of the ovum (2, 3). Soon it begins to move towards the female pro-nucleus, and reaching this the two become blended and a new nucleus is formed by their coalescence (4, 5). It is this nucleus, formed by the fusion of the male and female pro-nuclei, which initiates the division of the egg-cell and thus commences the development of the embryo.

Production of embryonic cells from the fertilized ovum, and their arrangement into layers.—Fertilization being completed, the ovum proceeds to divide into two daughter-cells (termed *segments* or *blastomeres*) in the same manner, and passing through the same phases,

as any other dividing cell. It is true that all the different forms of the nuclear fibres and the stages above described, in speaking of cell-division, have not been made out in the division of the egg-cell, but enough has been seen to warrant the assumption that the process is in the main the same. The result is, however, somewhat different, for in the mammalian ovum the two daughter-cells are not perfectly similar : one of them is larger, clearer, and, as the sequel shows, possessed of greater developmental activity than the other one, which is smaller and more granular. We may provisionally term the former the *ectomere* and the latter the *entomere* (fig. 17, *a*). The segmentation into two cells is soon followed by the division of each of these so that four are produced (fig. 17, *b*), and the process of multiplication being continued with more or less regularity a small solid mass of cells eventually results from the division

Fig. 17.

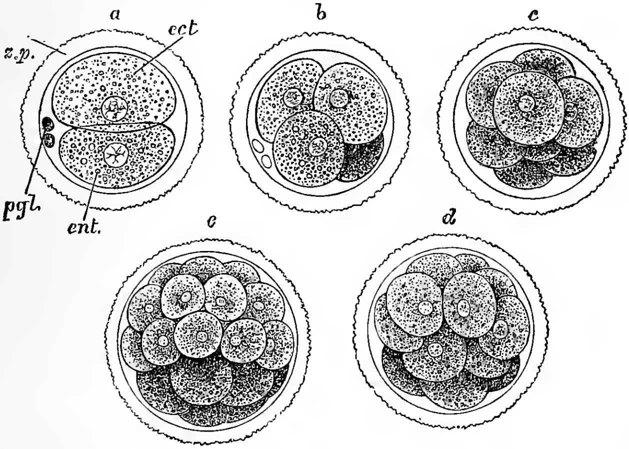

Fig. 17.—First stages of segmentation of a mammalian ovum : semi-diagrammatic (Drawn by Dr. Allen Thomson, after Ed. v. Beneden's description).

z.p., zona pellucida ; *p.gl.*, polar globules ; *ect.*, ectomere ; *ent.*, entomere. *a*, division into two blastomeres ; *b*, stage of four blastomeres ; *c*, eight blastomeres, the ectomeres partially enclosing the entomeres ; *d*, *e*, succeeding stages of segmentation showing the more rapid division of the ectomeres and the enclosure of the entomeres by them.

of the egg-cell (fig. 17, *e*, and fig. 18, *a*). Presently fluid tends to accumulate in the interior of the mass (fig. 18, *b*), transforming it into a hollow vesicle which is termed the *blastodermic vesicle* (fig. 18, *c*, *d*). The wall of this is formed by only a single layer of flattened cells (*ect.*), except at one part where there is a small patch of granular cells (*ent.*) constituting another but an imperfect layer, which, however, before long extends around the whole vesicle. A third or intermediate layer (derived from one or both the others) makes its appearance between the two which are first formed so that the blastoderm is finally tri-laminar. The outermost of the three blastodermic layers is termed the *ectoderm* or *epiblast*, the innermost, the *entoderm* or *hypoblast*, while the intermediate layer is the *mesoderm* or *mesoblast* (see fig. 20).

The result then of the division of the ovum is the production of

Fig. 18.

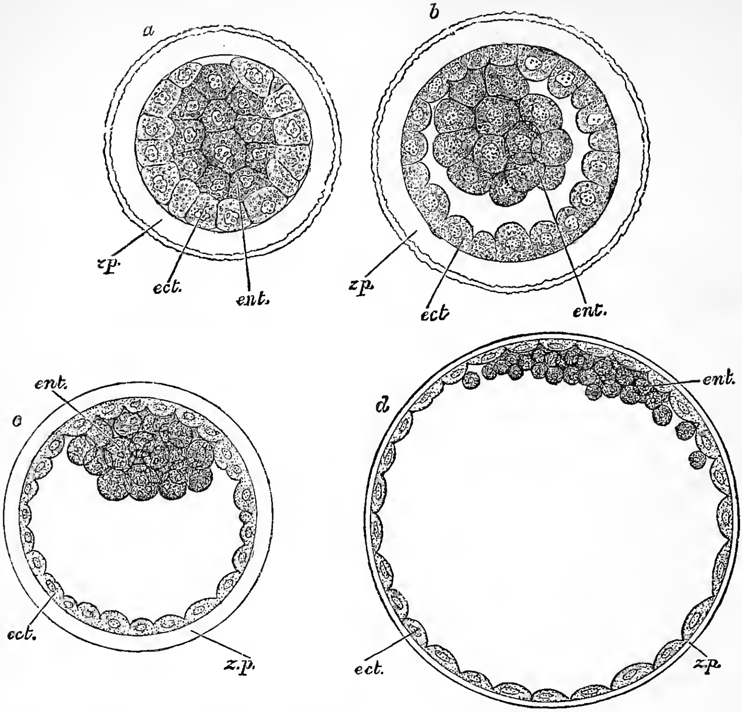

Fig. 18.—Sections of the ovum of the rabbit during the later stages of segmentation, showing the formation of the blastodermic vesicle (E. v. Beneden).

a, Section showing the enclosure of entomeres by ectomeres except at one spot—the blastopore; *b*, more advanced stage in which fluid is beginning to accumulate between entomeres and ectomeres, the former completely enclosed; *c*, the fluid has much increased, so that a large space separates entomeres from ectomeres except at one part; *d*, blastodermic vesicle, its wall formed of a layer of ectodermic cells, with a patch of entomeres adhering to it at one part; *z.p.*, *ect.*, *ent.*, as before.

A Fig. 19.

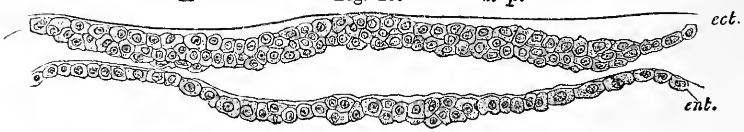

Fig. 20.

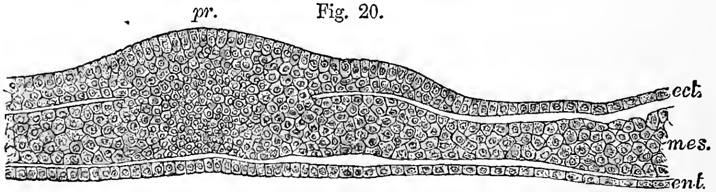

Fig. 19.—A. Section through part of a bilaminar blastoderm of the cat (E.A.S.) *ect.*, *ent.*, ectoderm, entoderm; *z.p.*, thinned out zona pellucida.

Fig. 20.—Section of trilaminar blastoderm of the rabbit (Kölliker). *ect.*, *ent.*, as before; *mes.*, mesoderm continuous in middle (*pr.*) with ectoderm.

numerous cells (embryonic cells), which are arranged in the three definite layers above enumerated. From these embryonic cells and their descendants the various tissues of the body eventually become formed. This development of the tissues or "histogenesis" does not take place promiscuously, but there is a certain relation maintained between the several layers of the blastoderm, and certain tissues; that is to say, some tissues are always formed from cells belonging to one layer, others from cells belonging to another. The following is the relation, given in tabular form :—

Ectoderm or Epiblast	Nervous tissue. The epithelium of the sense organs. The epithelium of the central canal of the spinal cord and of the ventricles of the brain. The epithelium of the skin (epidermis). The epithelium of the mouth.
Entoderm or Hypoblast	The epithelium of the alimentary canal (except the mouth) and of the glands in connexion with it.
Mesoderm or Mesoblast	The renal epithelium. The epithelium of vessels and serous membranes. The connective tissues (including cartilage and bone). Muscular tissue.

OF THE NUTRITION AND GROWTH OF CELLS.

When a cell divides, the resulting cells, as we have seen, are smaller than the original cell; but they speedily grow, and each of the daughter-cells before long attains the size of the mother-cell. In order to enable cells thus to grow or increase in size, they are supplied with nutritive material, which, under ordinary circumstances is immediately derived from the plasma of the blood, which transudes through the coats of the small blood-vessels, and thus reaches the elements of the tissues. It is in all cases a necessary condition that this material of nutrition should be brought within reach of the spot where nutrition goes on, although it is not essential for this purpose that the vessels should actually pass into the tissue.

In the instance of cuticle and epithelium, no vessels enter the tissue, but the nutrient fluid which the subjacent vessels afford penetrates a certain way into the growing mass, and the cells continue to assimilate this fluid, and undergo their changes at a distance from, and independently of, the blood-vessels. In other non-vascular tissues, such as articular cartilage, the nutrient fluid is doubtless, in like manner, conveyed by imbibition through their mass, where it is then attracted and assimilated. The mode of nutrition of these and other non-vascular masses of tissue may be compared, indeed, to that which takes place throughout the entire organism in cellular plants, as well as in those simple kinds of animals in which no vessels have been detected. But even in the vascular tissues the conditions are not absolutely different; for although the vessels traverse the tissue, they do not penetrate into its structural elements. Thus the capillary vessels of muscle pass between and around its fibres, but do not penetrate their inclosing sheaths. The nutrient fluid, on exuding from the vessels, has here, therefore, as well as in the non-vascular tissues, to permeate the adjoining mass by transudation, in order to reach these elements, and yield new substance at every point where renovation is going on. The vessels of a tissue have, indeed, been not unaptly compared to the artificial channels of irrigation which distribute water over a field; just as the water penetrates and pervades the soil which lies between the intersecting streamlets, and thus reaches the growing plants, so the nutritious fluid, escaping through the coats of the blood-vessels, must permeate the interme-

diate mass of tissue which lies in the meshes of even the finest vascular network. The quantity of fluid supplied, and the distance it has to penetrate beyond the vessels, will vary according to the proportion which the latter bear to the mass requiring to be nourished.

By its growth taking place more in one direction than another, a cell becomes modified in shape. Of course, if a cell, originally spherical, grows equally in all directions, the spherical form is maintained, except in those cases where, by mutual compression the cells acquire flattened sides and a polyhedral shape. If the cell grows out very much more in one direction than in others, a fibre may be formed, as in the production of nerve-fibres ; or, if a cell thus produced becomes hollowed out and united with other similar cells, a vessel may result, as in the production of blood-vessels. By the growth of a cell at several different points or by its retraction between certain points, a stellate form is produced; and, indeed, innumerable instances might be given of modifications in the shape of cells produced by inequalities in growth.

One of the modifications in shape produced by compression has just been referred to. Another instance is seen in those cases in which, by the continual division and growth of deeper lying cells, other cells, which are placed more superficially, become flattened out and forced towards the surface, as happens in the case of the stratified epithelia.

Waste of the tissues.—The tissues and organs of the animal body, when once employed in the exercise of their functions, are subject to continual loss of material, which is restored by nutrition. This waste or consumption of matter, with which in all cases the use of a part is attended, takes place in different modes and degrees in different structures. Thus in the cuticle the decayed parts are thrown off at the free surface; in the vascular tissues, on the other hand, the old or effete matter must be first reduced to a liquid state, then find its way into the blood-vessels, or lymphatics, along with the residual part of the nutritive plasma, and be by them carried off.

Regeneration.—When a part of a texture has been lost or removed, the loss may be repaired by regeneration of new substance of the same kind; but the extent to which this restoration is possible is very different in different textures. The special circumstances of the regenerative process in each tissue will be considered hereafter ; but we may here state generally, that, as far as is known, the reproduction of a texture is effected in the same manner as its original formation.

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Jan 29.

THE BLOOD.

The most striking external character of the blood is its well-known colour, which is bright red approaching to scarlet in the arteries, but of a dark purple or modena tint in the veins. It is a somewhat clammy and consistent liquid, a little heavier than water, its specific gravity being about 1·055; it has a saltish taste, a slight alkaline reaction, and a peculiar faint odour.

To the naked eye the blood appears opaque and homogeneous; but, when examined with the microscope, either while within the minute vessels, or when spread out into a thin layer upon a piece of glass, it is seen to consist of a transparent colourless fluid, named the "lymph of the blood," "liquor sanguinis," or "plasma," and minute solid particles or corpuscles immersed in it. These corpuscles are of two kinds, the coloured and the colourless: the former are by far the more abundant, and have been long known as "the red particles," or "globules," of the blood; the "colourless," "white," or "pale corpuscles," on the other hand, being fewer in number and less conspicuous, were later in being generally recognised.

When blood is drawn from the vessels, the liquor sanguinis separates into two parts;—into fibrin, which becomes solid, and a pale yellowish liquid named *serum*. The fibrin in solidifying involves the corpuscles and forms a red consistent mass, named the clot or *crassamentum* of the blood, from which the serum gradually separates. The relation between the above-mentioned constituents of the blood in the liquid and the coagulated states may be represented by the subjoined scheme:—

$$\text{Liquid blood}\left\{\begin{array}{l}\text{Corpuscles . . . .} \\ \text{Liquor sanguinis}\left\{\begin{array}{l}\text{Fibrin . .} \\ \text{Serum . .}\end{array}\right.\end{array}\right. \qquad \left.\begin{array}{l}\left.\begin{array}{l}\text{Corpuscles}\\ \text{Fibrin}\end{array}\right\}\text{Clot}\\ \text{Serum}\end{array}\right\}\text{Coagulated blood.}$$

In a cubic millimeter of healthy human blood there are on an average 5,000,000 red corpuscles (Vierordt) and 10,000 white corpuscles. The number of white corpuscles varies much more than that of the red, and the proportion of the white to the red is variously given at from 1 : 1000 to 1:250. There are said to be fewer red corpuscles in the female (4,500,000 in a cubic millimeter according to Welcker).

The numeration of the blood-corpuscles is readily performed. A little blood, obtained by pricking the finger, is measured in a capillary tube, and is then mixed with a measured amount (say 100 times its volume) of dilute solution of sulphate of soda, or some other salt which will maintain its fluidity and at the same time preserve the corpuscles nearly unaltered; the latter can then be counted in a small known quantity of the mixture. This part of the operation is effected by placing a drop of the mixture in the middle of a glass "cell" of a certain depth (say $\frac{1}{10}$th of a millimeter), the bottom of which is ruled in squares, the sides of which are of a known dimension (say again $\frac{1}{10}$ mill.). If now a covering glass is placed over the cell so as to touch the drop, the latter will form a layer of the mixture $\frac{1}{10}$ mill. deep, and the part above each square will represent a cube of liquid the sides of which measure $\frac{1}{10}$ mill. So that by counting the number of corpuscles in a square, after allowing them time to subside, the number in this

volume of the mixture is obtained. It is clear that a simple calculation will then give the number in a cubic millimeter of the blood employed.

The methods of Hayem and Nachet, Gowers, and Thoma are based on the above principle. The average results obtained by recent investigators agree closely with the original estimates of Vierordt and Welcker.

RED CORPUSCLES OF THE BLOOD.

These are not spherical, as the name "globules," by which they were formerly designated, would seem to imply, but flattened or disk-shaped. Those of the human blood (fig. 21 and fig. 22, A) have a nearly circular outline, like a piece of coin, and most of them also present a shallow cup-like depression or dimple on both surfaces; their usual figure is, therefore, that of biconcave disks. Their magnitude differs somewhat even in the same drop of blood, and it has been variously assigned by authors; but the prevalent size may be stated at from $\frac{1}{3500}$th to $\frac{1}{3200}$th of an inch (·007 to ·008 millimeter)* in diameter, and about one-fourth of that in thickness.

Fig. 21.

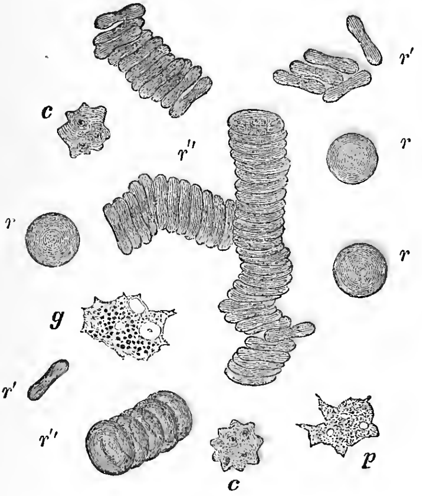


Fig. 21.—Human blood as seen on the warm stage. Magnified about 1200 diameters (E. A. S.).

r, *r*, single red corpuscles seen lying flat; *r'*, *r'*, red corpuscles on their edge and viewed in profile; *r''*, red corpuscles arranged in rouleaux; *c*, *c*, crenate red corpuscles; *p*, a finely granular pale corpuscle; *g*, a coarsely granular pale corpuscle. Both have two or three distinct vacuoles, and were undergoing changes of shape at the moment of observation; in *g*, a nucleus also is visible.

In mammiferous animals generally, the red corpuscles are shaped as in man, except in the camel tribe, in which they have an elliptical outline. In birds, reptiles, amphibia, and most fishes, they are oval disks with a central elevation on both surfaces (fig. 22, B, and fig. 27, from the frog), the height and extent of which, as well as the proportionate length and breadth of the oval, vary in different instances, so that in some fishes the elliptical form is almost shortened into a circle.

The size of the corpuscles differs greatly in the different classes of Vertebrata; they are largest in the Amphibia. Thus in the frog they are about $\frac{1}{1000}$th of an inch long and $\frac{1}{1700}$th broad; in Proteus anguinus, $\frac{1}{400}$th of an inch long and $\frac{1}{727}$th broad: in Amphiuma tridactylum, where they are largest, the red corpuscles are one-third larger than those of the Proteus. In birds they range in length from about $\frac{1}{2100}$th to $\frac{1}{1700}$th of an inch. Amongst mammals the elephant has the largest red blood-corpuscles ($\frac{1}{2700}$th of an inch); those of the dog average $\frac{1}{3500}$th of an inch; those of the sheep $\frac{1}{5000}$th of an inch; the goat was long supposed

* The one-thousandth part of a millimeter is often known as a *micro-millimeter* or *micron*, and is represented by the Greek letter μ. The diameter of a red blood corpuscle is then expressed as 7—8 microns ($7\ \mu$—$8\ \mu$).

to have the smallest, ($\frac{1}{6400}$th of an inch) but Gulliver found them about half this size in the Meminna and Napu deer.

In observations upon the blood of different races of mankind, Richardson found no constant difference, the average diameter of the red blood-corpuscle being $\frac{1}{3224}$th of an inch. The corpuscles of many mammals, and notably the dog among the common domestic animals, approach so nearly in size to the human blood-corpuscles as to be quite undistinguishable from them.

Fig. 22.

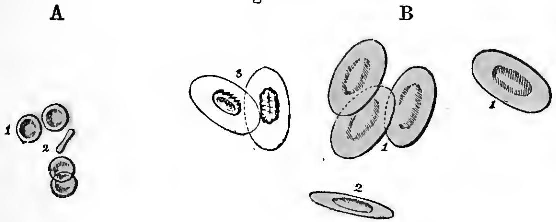


Fig. 22.—Human red corpuscles (A) and blood corpuscles of the frog (B) placed side by side to show relative size. 500 diameters.

1, shows their broad surface; 2, one seen edgeways; 3, shows the effect of dilute acetic acid; the nucleus has become distinct (from Wagner).

When viewed singly by transmitted light the coloured corpuscles do not appear red, but merely of a reddish-yellow tinge, or yellowish-green in venous blood. It is only when the light traverses a number of corpuscles that a distinct red colour is produced.

In consequence of the shape of the corpuscle, it looks darker in the middle than at the edge when viewed with only a moderate magnifying power, or at a distant focus; but the middle of the corpuscle appears lighter than the periphery when a close focus or a very high magnifying power is employed.

The red disks, when blood is drawn from the vessels, sink in the plasma; they have a singular tendency to run together, and to cohere by their broad surfaces, so as to form by their aggregation cylindrical columns, like piles or rouleaus of money, and the rolls or piles themselves join together into an irregular network (figs. 21 and 23). Generally the corpuscles separate on a slight impulse, and they may then unite again. The phenomenon is most readily explained by supposing the substance composing the corpuscles to possess a slight natural adhesiveness (Lister). It will take place in blood which has been in any way brought to a standstill within the living vessels as well as in blood that has stood for some hours after it has been drawn, and also when the globules are immersed in serum in place of liquor sanguinis.

Fig. 23.

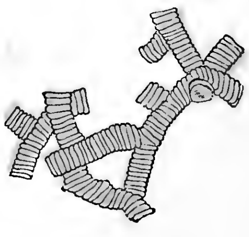


Fig. 23.—Red corpuscles collected into rolls (after Henle).

The corpuscles alter their shape on the slightest pressure, as is well

seen while they move within the vessels; they are also elastic, for they readily recover their original form.

The human blood-corpuscles, as well as those of the lower animals, often present deviations from the natural shape, which are most probably due to causes acting after the blood has been drawn from the vessels, but in some instances depend upon abnormal conditions previously existing in the blood. Thus, it is not unusual for many of them to appear shrunken and crenated, when exposed under the microscope (fig. 21, *c*, *c*; fig. 24, *f*), and the number of corpuscles so altered often appears to increase during the time of observation. This is, perhaps, the most common change; it occurs whenever the density of the plasma is increased by the addition of a neutral salt, and is one of the first effects of the passage of an electric shock. The corpuscles may become distorted in various other ways, and corrugated on the surface; not unfrequently one of their concave sides is bent out, and they acquire a cup-like figure.

Gulliver made the curious discovery that the corpuscles of the Mexican deer and some allied species present very singular forms, doubtless in consequence of exposure; the figures they assume are various, but most of them become lengthened and pointed at the ends, and then often slightly bent, not unlike caraway-seeds.

Structure of the coloured blood corpuscles.—Each red corpuscle is formed of two distinct parts, a coloured and a colourless, but under ordinary circumstances the two are intimately commingled, so that every portion of the corpuscle, however small, has to all appearance the same constitution: the corpuscles therefore look homogeneous.

Of the two parts composing the corpuscle the one which imparts its colour to the blood-disk consists of a red crystallizable substance termed *hæmoglobin*, the colourless part is termed the *stroma*. Hæmoglobin is readily soluble in water, and the addition of this fluid to a drop of blood serves speedily to separate the coloured substance from the colourless part of the corpuscle (fig. 24, *a*—*e*). The same effect, namely,

Fig. 24.

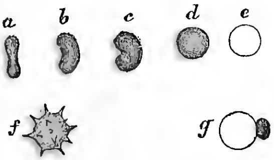


Fig. 24.—*a*–*e*, successive effects of water upon a red blood-corpuscle; *a*, corpuscle seen edgeways, slightly swollen; *b*, *c*, one of the sides bulged out (cup form); *d*, spherical form; *e*, decolorized stroma; *f*, a thorn-apple shaped corpuscle (due to exposure); *g*, action of tannin upon a red corpuscle.

the discharge of colouring matter from the corpuscles, may be produced by various other means, such as the action of heat (60° C.), the alternate freezing and thawing of a portion of blood, the action of ether and chloroform vapour, and the passage of electric shocks through blood; in these cases the hæmoglobin becomes dissolved by the serum. Many watery solutions, such as dilute acids, act like water itself. The effect of a solution of tannic acid is peculiar, from the fact that the hæmoglobin, although discharged from the corpuscle, yet being insoluble in the solution, is immediately precipitated upon the surface of the stroma in the form of a small darkly coloured globule (Fig. 24, *g*.) (W. Roberts).

The blood or serum of many animals belonging to different genera

cannot be mixed without producing the decolorization and destruction of the red corpuscles of one or both sorts of blood (Landois).

Blood in which the hæmoglobin has been dissolved out from the corpuscles by any of these means is seen to have lost its opaque appearance, and to have acquired a transparent laky tint; the change depends upon the fact that the colouring matter when dissolved in the serum and forming a homogeneous layer, interferes less with the transmission of light than when occurring in scattered particles.

Hæmoglobin after being thus separated from the blood-corpuscles is prone to undergo crystallization. The crystals present various forms in different animals, but almost all (the hexagonal plates of the squirrel being alone excepted) belong to the rhombic system. From human blood and that of most mammals, the crystals are elongated prisms (fig. 25, 1), but they are tetrahedrons in the guinea-pig (2), and short rhombohedrons in the hamster (4). They are most readily obtained for microscopical examination from the blood of the rat, where they appear merely on the addition of a little water.

Fig. 25.

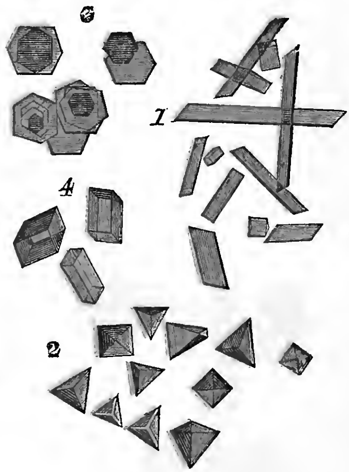


Fig. 25.—Blood-crystals, magnified.

1, from human blood; 2, from the guinea-pig; 3, squirrel; 4, hamster.

All hæmoglobin crystals contain a certain amount of water of crystallization (Kühne). They are doubly refracting (anisotropous). The spectrum of hæmoglobin, whether in substance or in solution, may be always readily recognized by the double or single absorption bands, which are produced according as it is present in the oxidated or deoxidated condition (Stokes).

Other coloured crystals, which may be obtained from blood, are the so-called "hæmin crystals" of Teichmann. They are formed when hæmoglobin is warmed with a little salt and glacial acetic acid. On cooling, the hæmin crystallizes out in minute reddish-brown acicular prisms (fig. 26), the demonstration of which affords a positive proof of the presence of blood-colouring matter. They may readily be obtained from dried blood without the addition of salt, merely by warming it with concentrated acetic acid.

Fig. 26.

Fig. 26.—Hæmin crystals, magnified (from Preyer).

The amount of hæmoglobin in each corpuscle, which is liable to variation, may be approximately arrived at by determining both the number of corpuscles and the amount of hæmoglobin in a given volume of blood. The amount of hæmoglobin is estimated by diluting a sample of blood with a known amount of water, and comparing the tint of the solution so obtained with that of a solution of hæmoglobin of known strength. A very convenient means of quickly obtaining an idea of the amount of hæmoglobin in a sample of blood is afforded by the "hæmoglobinometer" of Gowers, which is arranged on the above principle.

The stroma of the red corpuscle during the removal of the hæmoglobin generally loses its discoid shape and becomes globular. It is itself composed of a number of chemical substances, chief among which are paraglobulin, cholesterin, and protagon.

STRUCTURE OF THE NUCLEATED RED CORPUSCLES OF THE LOWER VERTEBRATA.

Like the mammalian blood-discs the large corpuscles of the frog (fig. 27) and salamander, may be described as consisting of coloured substance and stroma. They differ from the mammalian corpuscles, however, in the possession of a more solid particle of an oval shape which lies imbedded in the stroma, and has been long known as the "nucleus." It is rather more than one-third the length of the corpuscle, but in the natural unaltered condition is seldom visible; this is probably owing to the fact that it possesses very nearly the same index of refraction as the rest of the corpuscle. For it may be rendered visible, even under such circumstances, by the combined action of watery vapour and carbonic acid upon the blood; a precipitate (of paraglobulin) is thus produced upon the nucleus, and its outline comes into view: on readmission of air the precipitate is re-dissolved, and the nucleus again becomes faint or disappears (Stricker).

The effect of most reagents is similar to that produced on human blood. Water causes both stroma and nucleus to swell up by imbibition, the coloured part being at the same time extracted. A dilute solution of acetic acid in an indifferent fluid also removes the colouring matter, but the stroma and nucleus retain their shape, the last-mentioned body presenting a markedly granular appearance (fig. 22, 3); if strong acetic acid be employed, the nucleus often acquires a reddish tint. Alkalies, on the other hand, even when very dilute, rapidly destroy both corpuscle and nucleus. Various reagents added to newt's blood cause the coloured part of the corpuscles to become gradually withdrawn from the stroma, and collected around the nucleus; this is especially the case with a two per cent. solution of boracic acid (Brücke): the coloured matter and nucleus ("zooid") may subsequently be altogether extruded from the body of the corpuscle ("oecoid").

Fig. 27.

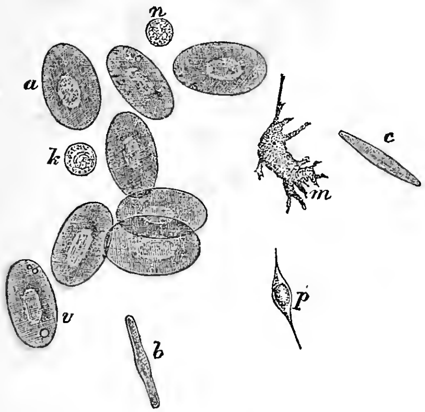


Fig. 27.—Frog's blood (Ranvier).

a, red corpuscle seen on the flat; *v*, vacuole in a corpuscle; *b*, *c*, red corpuscles in profile; *n*, pale corpuscle at rest; *m*, pale corpuscle, exhibiting amœboid movements; *p*, coloured fusiform corpuscle.

Dilute alcohol brings to view one, or at most two, nucleoli within the nucleus of the amphibian red corpuscle (Ranvier, Stirling). In other respects also this structure resembles the nucleus of an ordinary cell, for it contains a network traversing its interior (fig. 28), which is, however, very close, and produces under moderate powers of the microscope a somewhat granular effect. It is doubtful whether the nucleus of the adult corpuscle can undergo division, although in the young state the division of the nucleus, followed or accompanied by that of the corpuscle, has frequently been observed.

A question which has been much discussed, is as to the existence of a membrane or cell-wall around the red corpuscle. The effects of the action of water and of a solution of salt respectively, seem in favour of the view that

such a membrane is present. The addition of water to the blood, causes the corpuscles, both those of man and of the frog, to lose their flattened shape and to become spherical; and since this change will occur long after the blood has been drawn, and cannot, for this and other reasons, be referred to the existence of contractility in the corpuscle, there is only one explanation which can be offered; namely, that water has passed into the corpuscle by osmosis, and has thus distended the corpuscle. In the same way the action of salt, in causing a crenation of the corpuscle, can be best explained by supposing that watery fluid has passed out from the corpuscle by osmosis, so that the superficial layer which envelopes the rest of the corpuscle is thrown into folds or creases. But it is not necessary to suppose that this enveloping layer is of the nature of a distinct membrane; for if we assume that the substance of the corpuscle has a more fluid consistence internally than near the exterior, a sufficient explanation of the phenomena resulting both from the action of water and of salt is obtained without asserting the existence of a definite membrane, a structure which no one has succeeded in demonstrating in an isolated form.

Fig. 28.

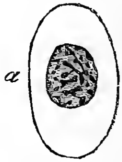


Fig. 28.—Coloured corpuscle of salamander, showing intra-nuclear network (Flemming).

Gaule has recently described the development under certain conditions within the red corpuscles of the frog of a minute organism which subsequently escapes from the corpuscle, and moves actively about in the surrounding fluid. Gaule is of opinion that the organism in question is formed out of the living substance (protoplasm, zooid) of the red corpuscle, and is an active free condition of this. It would seem, however, to be far more probably of a parasitic nature, developed from a minute invisible germ that had lain latent within the corpuscle, ready to undergo development under favourable conditions.

Under the influence of certain conditions (heat, presence of septic material) and reagents (urea solution, dilute sherry wine), the coloured blood-corpuscles often extrude fine beaded filaments which may attain a considerable length, and undergo varied changes. As Dowdeswell has correctly pointed out, these filamentous extrusions militate decidedly against the existence of a membranous envelope to the corpuscle. It is not by any means proven, however, that the filaments are protoplasmic in nature, like the amœboid processes of the colourless corpuscles, for it is possible to explain their occurrence by supposing that they are caused by the action of the fluid upon the protagon in the stroma, much in the same way as the well-known "myelin figures" are formed from the protagon in the white substance of nervous tissue when this is submitted to the action of water.

The affirmation of Böttcher that a nucleus is present in the mammalian red blood-corpuscle, rests entirely upon erroneous methods of preparation. That of Stricker (which is a revival of the older opinions of Wharton Jones, and of Busk and Huxley) that the mammalian red corpuscle is morphologically a nucleus with an imperceptible amount of enveloping cell-substance, is quite distinct from Böttcher's view, and has certain considerations to recommend it, but is supported, at present upon an insufficient basis of fact, and is opposed, moreover, to recent observations upon the development of the red disk.

COLOURLESS CORPUSCLES OF THE BLOOD.

General Characters.—The white, pale, or colourless corpuscles are few in number as compared with the red, and both on this account and because of their want of colour, they are not at first easily recognized in a microscopic preparation of blood. Their form is very various, but when absolutely at rest they are rounded or spheroidal. Measured in this condition they are found to be about $\frac{1}{2500}$th of an inch (.001 mm.) in diameter. They are specifically lighter than the red corpuscles.

The white corpuscle may be taken as the type of a free animal cell. It is a minute protoplasmic structure inclosing one or more nuclei, and the protoplasm, being to all appearance unaltered from its primitive condition, and unenclosed in a definite membrane or cell-wall, is capable of exhibiting in a high degree the amœboid movements and other phenomena which depend upon the possession of contractility and have been already sufficiently described. The white blood-corpuscles are peculiarly apt to

Fig. 29.

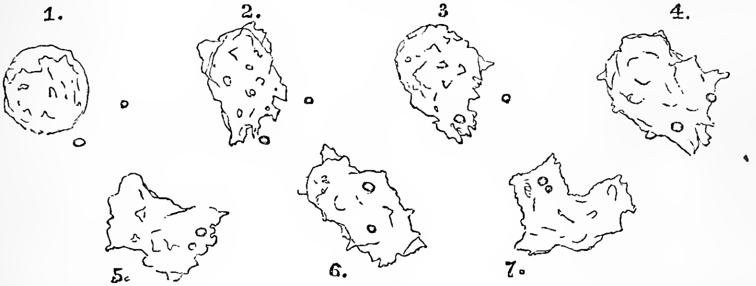


Fig. 29.—Changes of form of a white corpuscle of newt's blood, sketched at intervals of a few minutes. The figures show also the intussusception of two small starch granules, and the changes of position which these underwent within the corpuscle. (E. A. S.)

take into their interior minute solid particles that have been introduced into the blood (fig. 29) ; this property has served in the hands of Cohnheim and others as a means of detecting escaped white corpuscles in tissues which are wholly extravascular, such as the cornea. Some of the colourless corpuscles have in their protoplasm a number of comparatively coarse round granules (fig. 21, *g*) which are generally grouped together round the nucleus. These corpuscles are often distinguished from the more common paler variety, (fig. 21, *p*) as the coarsely granular cells, but it has not been shown that they are different in nature, origin, or destination.

Both coarsely granular and finely granular corpuscles are often seen, which are much smaller than the ordinary pale cells, consisting chiefly of a spheroidal nucleus with but little surrounding protoplasm. They seem to be young forms of the more protoplasmic corpuscles, and are perhaps identical with the lymphoid cells found in lymphatic glands and similar structures.

The corpuscles often have one or more conspicuous vacuoles in their protoplasm, but these are inconstant, and may appear and disappear in the same corpuscle. More rarely they are filled with vacuoles so that the cell-substance assumes a frothy aspect. This is commoner in the white blood-corpuscles of the newt and other cold-blooded animals than in those of man. By means of the amœboid movement of their protoplasm, the pale corpuscles, under some circumstances, possess the power of wandering or emigrating from the blood-vessels, penetrating between the elements of their coats, and in this manner they find their way into the interstices of the tissues, and hence into the commencements of the lymphatics. Cells like these which appear to be wandering independently in the tissues, and particularly in the connective tissue, are known as *migratory cells*.

Besides the two forms of pale corpuscles previously referred to, others have been described which differ from them in containing red-coloured granules in their protoplasm. According to A. Schmidt and Semmer, such cells are very numerous in the circulating blood, but on withdrawal of the blood from the vessels they become rapidly destroyed and disappear without leaving a trace. Schmidt looks upon them as transitional forms between the white and red corpuscles, but the evidence of their constant occurrence in normal blood is at present unsatisfactory.

The pale corpuscles possess one, two, or more nuclei, which are generally obscure in the living condition, but are occasionally seen when the cor-

Fig. 30.

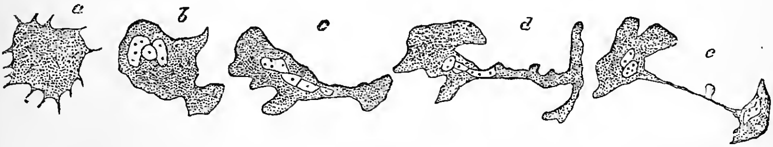
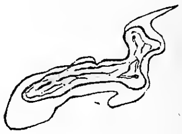


Fig. 30.—A PALE CORPUSCLE OF THE NEWT'S BLOOD WITH THREE NUCLEI (Klein). *a*—*e*, successive forms assumed at intervals of a few minutes.

puscle becomes flattened out (fig. 30, *b*, *e*,) and may always be brought into view by reagents. The nuclei are apt to take on peculiar shapes, caused perhaps by traction exercised upon them by the movements of

Fig. 31.—A PALE CORPUSCLE OF THE SALAMANDER, SHOWING ELONGATED IRREGULAR NUCLEUS WITH INTRANUCLEAR NETWORK. (Flemming.)

Fig. 31.



the surrounding protoplasm. Thus a nucleus not-unfrequently becomes elongated and either irregular in outline (fig. 31) or folded on itself, so that when the ends are turned up, the appearance of two nuclei is produced, where in reality there may be but one. In other respects they have the normal structure and appearance of cell-nuclei, containing the usual intranuclear network. The division of the nucleus and of the corpuscles takes place in the same way as in other animal cells, but it is probable that the phases are neither so numerous nor so complicated. The process, as observed in the newt's corpuscle, is as follows:—The nucleus becomes enlarged and transformed into a system of parallel fibres. The substance of the fibres gradually collects towards the two poles of the elongated nucleus, leaving the middle clear or bridged across only by fine filaments, while at each pole a new nucleus becomes formed. This is followed by a constriction of the protoplasm into two equal parts, which are collected around the two new nuclei. The change is accompanied by a radial arrangement of the granules in the protoplasm, the lines of granules converging towards the new nuclei.*

In some cases it would seem that the separation of the protoplasm may not occur until some time after the division of the nucleus has been completed; for white corpuscles are often seen containing two or more

* The changes of the nucleus have also been seen in the white corpuscles of the Salamander by Peremeschko.

nuclei, and such corpuscles have been observed to separate into two parts, each part taking with it a nucleus (Klein).

Action of Reagents.—Water swells up and destroys the protoplasm of the white corpuscles, setting free the granules. If but little water be mixed with the drop of blood, the protoplasm may not be destroyed, but the corpuscles are swollen out (fig. 32, 1), and the granules take on an active Brownian movement. Acetic acid causes a granular precipitate in the protoplasm, the granules collecting around the nucleus, which is brought very strongly into view (fig. 32, 2, 3). A

Fig. 32.

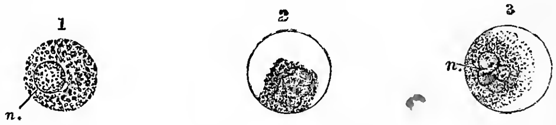


Fig. 32.—Colourless corpuscles treated with water and with acetic acid. (E.A.S.)

1, first effect of the action of water upon a white blood-corpuscle; 2, 3, white corpuscles treated with dilute acetic acid; *n.* nucleus.

clear bleb-like swelling is also generally produced from one or more sides of the corpuscle; but this appearance is not peculiar to acids, for it is often seen as an accompaniment of the death of the corpuscle, whether as the result of the action of reagents or from any cause. If produced by a solution of iodine, the blebs sometimes become coloured of a faint port wine tint, a reaction which is generally taken as an indication of the presence of glycogen.

In the blood of the splenic vein, and also in some other parts, cells have been noticed resembling pale corpuscles in their structure, but much larger, and enclosing in their protoplasm a number of red corpuscles, or in some cases partially disintegrated portions of red corpuscles. These are supposed to be pale cells which have taken in some of the red corpuscles, a process which appears to occur normally in the spleen itself.

Other microscopic elements in blood.—In the clear fluid which intervenes between the corpuscles, and which, in a preparation which has been made a short time, consists of serum, there can generally be detected a network of fine interlacing filaments of fibrin. There are also to be seen minute round colourless particles in this fluid, which become more evident after the preparation has been made for some time, or if the blood has been diluted with certain fluids. They are known as the *elementary particles* of Zimmermann, and especial attention has been lately drawn to them by Hayem, who re-describes them under the name "hæmatoblasts" as the source whence new red corpuscles are derived (see Development of Blood Corpuscles). Besides these scattered elementary particles, granular-looking masses (fig. 33), composed of exceedingly fine colourless particles, frequently occur in a drop of blood drawn from the finger, even when it is taken from a healthy person, but especially in cachectic states of the system. The particles are free in the circulating blood, but become massed together immediately that the blood is drawn (Osler). If one of the masses be observed for a time, at the temperature of the body, it may sometimes be seen that the minute particles composing it have grown out into or at least have become connected with delicate filaments which presently take on an oscillatory Brownian movement, by

virtue of which they eventually break away from the mass and become free in the surrounding liquid. According to Ranvier the filaments in question are fibrin-filaments.

Fig. 33.

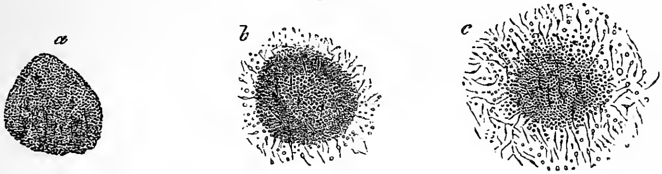


Fig. 33.—Granular mass of Max Schultze, observed in salt solution on the warm stage, showing the changes which it undergoes at its periphery. (Osler).

If blood be taken from an animal during digestion, especially of a meal containing much fatty food, the serum or plasma has a milky aspect. This is due to the presence of innumerable fine fatty molecules which have been absorbed from the intestines and discharged with the chyle into the blood.

THE LYMPH AND CHYLE.

A transparent and nearly colourless fluid, named "lymph," is conveyed into the blood by a set of vessels distinct from those of the sanguiferous system. These vessels, which are named "lymphatics," from the nature of their contents, and "absorbents," on account of their reputed office, take their rise in nearly all parts of the body, and, after a longer or shorter course, discharge themselves into the great veins of the neck; the greater number of them previously joining into a main trunk, named the thoracic duct,—a long narrow vessel which passes in front of the vertebræ, and opens into the veins on the left side of the neck, at the angle of union of the subclavian and internal jugular; whilst the remaining lymphatics terminate in the corresponding veins of the right side. The absorbents of the small intestine carry an opaque white liquid, named "chyle," which they absorb from the food as it passes along the alimentary canal; and, on account of the milky aspect of their contents, they have been called the "lacteal vessels." But in thus distinguishing these vessels by name, it must be remembered that they differ from the rest of the absorbents only in the nature of the matter which they convey; and that this difference holds good only while digestion is going on; for at other times the lacteals contain a clear fluid, not to be distinguished from lymph. The lacteals enter the commencement of the thoracic duct, and the chyle mingling with the lymph derived from the lower part of the body, is conveyed along that canal into the blood. Both lacteals and lymphatics, in proceeding to their destination, pass into and out of certain small, solid and vascular bodies, named lymphatic glands, which have a special structure and internal arrangement, as will be afterwards described; so that both the chyle and lymph are sent through these glands before being mixed with the blood.

Thus much having been explained to render intelligible what follows, we may now consider the lymph and the chyle, which, as will be seen, are intimately related to the blood.

Lymph, when examined with the microscope, is seen to consist of a clear liquid with corpuscles floating in it. The liquid part—lymph-plasma—bears a strong resemblance in its physical and chemical constitution to the plasma of the blood. The lymph-corpuscles agree entirely in their characters with the pale corpuscles of the blood. They vary in number in lymph from different parts, being more numerous in that which has passed through the lymphatic glands than in the lymph which enters those

bodies, thus indicating the lymphatic glands as an important source of lymph-corpuscles. Many of the corpuscles found in lymph are of small size, consisting of a small amount of protoplasm and a relatively large nucleus, and thus resembling the lymphoid cells of lymphatic glands. These cells are far less actively amœboid than those which are larger and contain more protoplasm. Since the lymph is poured into the blood, the lymph-corpuscles are to be looked upon as constantly furnishing a fresh supply of pale corpuscles to that fluid.

Chyle consists as we have seen merely of lymph, to which are added some of the absorbed products of digestion. These are chiefly particles of fatty matter or minute oil-globules, some of which are of appreciable size, but the greater number are immeasurably small. Like the fatty globules suspended in milk, they give the chyle a similar milky aspect. These minute fatty particles were named collectively by Gulliver the "molecular base" of the chyle.

Corpuscles, like the ordinary lymph-corpuscles but with a reddish tinge, have been described in the lymph and chyle as well as in the blood, and red disks have also been noticed, but these may have got into the lymphatics accidentally through a rupture of the fine vessels.

Origin of the white blood-corpuscles and of the corpuscles of the lymph and chyle.—As to the origin of the lymph and chyle corpuscles, it may, in the first place, be observed that the greatly increased proportion of these bodies in the vessels which issue from the lymphatic glands, and the vast store of corpuscles having the same characters contained in the interior recesses of these glands, are unmistakeable indications that the glands are at least a principal seat of their production. They are, most probably, produced by division of parent corpuscles or cells contained in the glands, and in some measure also by further division of corpuscles thus produced after they have made their way into the lymphatic vessels. The corpuscles found sparingly both in chyle and lymph before passing the mesenteric glands may be in part formed in the lymphatic tissue met with in the alimentary mucous membrane and other parts of the body. Pale corpuscles also, which have migrated from the vessels, may find their way into the beginning of the lymphatics. In this way the presence of corpuscles in the lymph even before it has passed through the lymphatic glands is accounted for. Lymph-corpuscles are probably also produced in the spleen and in the thymus gland; and it is believed by some that they may also be formed by proliferation of connective tissue corpuscles. The corpuscles of the chyle and lymph are carried into the sanguiferous system and become the pale corpuscles of the blood, but some of the latter may pass directly from the lymphatic glands, spleen, and other organs containing lymphatic or lymphoid tissue into the blood-vessels which are supplied to those organs.

DEVELOPMENT OF THE RED BLOOD-CORPUSCLES.

Origin of the nucleated red blood-corpuscles of the embryo.—The first red blood-corpuscles are formed very early in embryonic life simultaneously with and in the interior of the first blood-vessels. They are developed in the mesoderm, in a circular area which surrounds the part of the blastoderm which is occupied by the developing body of the embryo. The area is known as the vascular area, and the first blood-vessels and blood-corpuscles are, therefore, formed outside the actual body of the embryo. The process of development is as follows:—

Those mesodermic cells in the vascular area which are concerned with the formation of vessels become extended into processes of varying length, which grow out from the cells in two or more directions. The cells become united with one another, either directly or by the junction of their processes, so that an irregular network of protoplasmic nucleated corpuscles is thus formed (fig. 34). Meanwhile

the nuclei become multiplied, and whilst the greater number remain grouped together in the original cell-bodies or nodes of the network, some are seen in the uniting cords. The nuclei which remain in the centre of the nodes accumulate, each one around itself, a small amount of the cell protoplasm. The corpuscles thus formed (*bl*) acquire a reddish colour, and the protoplasmic network in which they lie becomes vacuolated and hollowed out into a system of branched canals enclosing fluid, in which the nucleated coloured corpuscles float. The intercommunicating canals gradually become enlarged so as to admit of the passage of the

Fig. 34.

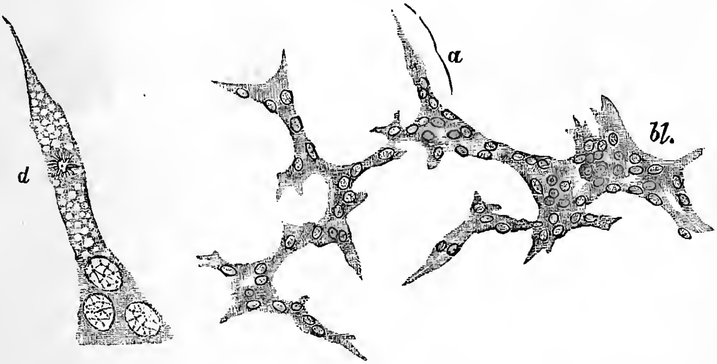


Fig. 34.—Part of the network of developing blood-vessels in the vascular area of the guinea-pig. (E. A. S.)

bl, blood-corpuscles becoming free in an enlarged and hollowed out part of the network. The smaller figure on the left represents *a* of the larger figure, more highly magnified ; *d*, a nucleus undergoing division.

corpuscles. The protoplasm which forms the wall of these first vessels becomes differentiated around the nuclei which have remained embedded in it, so as to give rise to the flat cells which compose the blood-capillaries.

As soon as the heart is developed, or even before this happens, the blood begins to move within the vessels of the vascular area. And when the action of the heart commences, it is driven also through vessels which are formed, probably in a similar manner, in the body of the embryo itself.

The first formed red blood-corpuscles are nucleated cells resembling the pale corpuscles except in their colour and in the clearness of their protoplasm, and, like the white corpuscles, they are capable of amœboid movement, and of undergoing multiplication by division. It is uncertain whether, as stated by Kölliker and others, any of the primary red blood-corpuscles are produced by direct transformation of individual cells of the mesoderm, but (whether by accession of some of these last, by division, or by a continuance of the original mode of formation), they increase considerably in number, and are soon accompanied by colourless corpuscles. These appear to be formed in great number in the embryonic liver as soon as this is developed, as well as in the lymphatic glands, spleen and thymus gland. It is generally supposed that the colourless corpuscles acquire colour, and are converted into nucleated red corpuscles, but there is no direct evidence in favour of this view.

The primary nucleated red corpuscles are at length succeeded by smaller disk-shaped red corpuscles without nuclei, having all the characters of the blood-disks of the adult. This substitution proceeds gradually, until, long before the end of intrauterine life, the *nucleated* red corpuscles have almost entirely vanished. According to Neumann, some are still to be met with even in the new-born child. It is uncertain whether the nucleated red corpuscles are converted into non-nucleated disks, or if they simply disappear as the red disks become formed.

Origin of the Red Blood-Disks.—1. Intracellular origin. The disk-shaped red corpuscles are produced in the interior of mesodermic or connective tissue cells in the following manner :—

A part of the protoplasm of the cell acquires a reddish tinge (fig. 35, *h*), and after a time the coloured substance becomes condensed in the form of globules (*h′*) within the cells, varying in size from a minute speck to a spheroid of the

Fig. 35.

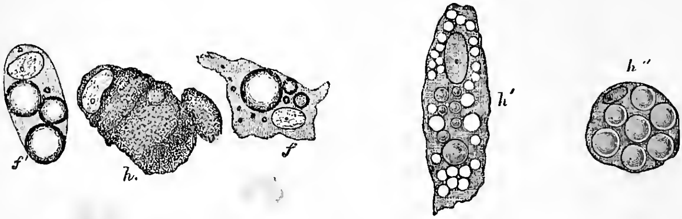


Fig. 35.—Development of red corpuscles in connective tissue cells. From the subcutaneous tissue of the new-born rat. (E. A. S.)

h, a cell containing hæmoglobin in a diffused form in the protoplasm ; *h′*, one containing coloured globules of varying size, and vacuoles ; *h″*, a cell filled with coloured globules of nearly uniform size ; *f*, *f′*, developing fat cells.

diameter of a blood-corpuscle, or even larger ; but gradually the size becomes more uniform (fig. 35, *h″*). Some parts of the embryonic connective tissue, especially where a vascular tissue, such as the fat, is about to be developed, are completely studded with cells like these, occupied by a number of coloured spheroids and forming nests of blood-corpuscles, or minute " blood-islands." After a time the cells become elongated and pointed at their ends, and processes grow out to join prolongations of neighbouring blood-vessels or of similar cells. At the same time vacuoles form within them (fig. 35, *h′*), and becoming enlarged coalesce to form a cavity filled with fluid, in which the reddish globules, which are now becoming disk-shaped, float (fig. 36). Finally the cavity extends through the cell processes into those of neighbouring cells, and a vascular net-work is produced, and this becomes eventually united with pre-existing blood-vessels, so that the blood-corpuscles which have been formed within the cells in the manner described, get into the general circulation (see Development of Blood-vessels).

Fig. 36.

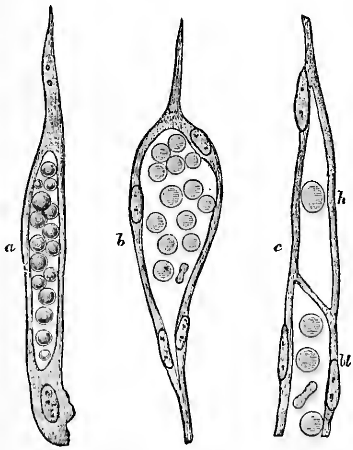


Fig. 36.—Further development of blood-corpuscles in connective tissue cells, and transformation of the latter into capillary blood-vessels. (E. A. S.)

a, an elongated cell with a cavity in its protoplasm occupied by fluid and by blood-corpuscles which are still globular ; *b*, a hollow cell the nucleus of which has multiplied. The new nuclei are arranged around the wall of the cavity, the corpuscles in which have now become discoid ; *c*, shows the mode of union of a " hæmapoietic " cell, which in this instance contains only one corpuscle, with the prolongation (*bl*) of a previously existing vessel. *a*, and *c*, from the new-born rat ; *b*, from a fœtal sheep.

This " intracellular " mode of development of red blood-corpuscles ceases in most animals before birth, although in those which, like the rat, are born very

immature, it may be continued for a few days after birth. Subsequently, although new vessels are formed in the same way, blood-corpuscles are not produced within them, and it becomes necessary to seek for some other source of origin of the red blood-disks, both during the remainder of the period of growth, and also during adult life, for it is certain that the blood-corpuscles are not exempted from the continual expenditure and fresh supply which affect all the other tissues of the body.

2. Origin from white corpuscles.—The view which long obtained most prevalence, and was supported by the opinions of Hewson, Wharton Jones, Kölliker, Paget, Busk and Huxley, and others, is that the red disks are developed from the white corpuscles, and the statements of A. Schmidt and of Semmer above mentioned (see p. 31), would seem to confirm this view. For if corpuscles are present in the blood which present transitional forms between the white and red corpuscles, it is probable that these are white corpuscles in process of transformation into red. There are, however, no other recorded observations of recent date which show conclusively that the red corpuscles are thus developed.

3. In the marrow of bones.—In the peculiar pale cells of the red marrow which fills the internal cavities of many bones, and particularly the ribs, appearances have been observed which justify the inference that red blood-corpuscles are here becoming developed. These appearances, in the shape of transitional forms between the marrow-cells and red corpuscles, were long ago described by Neumann, and by Bizzozero, and have been noticed also by other observers. The accounts are, however, somewhat different; for, according to Bizzozero, the *nucleus* of the marrow-cell becomes coloured, and with a small amount of protoplasm persists as the red disk, while Neumann described the *protoplasm* as becoming transformed into the red corpuscle whilst the nucleus disappears.

Observations which I have myself made on the red marrow of the guinea-pig have tended to confirm the view taken by Neumann, in that they have made evident that the colour of these so-called "transition-cells" is not situated in the nucleus, but chiefly if not entirely resides in the protoplasm; moreover the coloured cells that I have noticed have almost always been distinctly smaller than the ordinary marrow-cells, often of irregular forms, and sometimes appear as if undergoing division (fig. 37). They closely resemble, in fact, the nucleated red blood-corpuscles of the embryo, which may certainly thus multiply (by division), and it is not altogether improbable that the cells in question are descendants of the embryonic red blood-corpuscles, and not necessarily transition-forms between marrow-cells and the red blood-disks. By this opinion it is not intended to imply that blood-disks are not eventually produced from the coloured cells here spoken of.

Fig. 37.

Fig. 37.—Coloured nucleated cells from the red marrow of the guinea-pig. (E. A. S.)

Rindfleisch has recently given a detailed account of the manner in which such a production of red blood-disks is effected in the marrow, as follows:—

The marrow-cells, which are very like large pale blood-corpuscles, but with a less granular protoplasm and a larger more distinct nucleus, acquire a reddish tinge in consequence of the formation of hæmoglobin in the protoplasm. The colour becomes gradually more pronounced, and soon it is found that it is confined to a part only of the protoplasm. Presently the coloured protoplasm gradually becomes separated from the rest of the cell, and forms a red corpuscle which is at first cup-shaped, but afterwards becomes moulded in the circulation to form a biconcave disk. The protoplasm which is left in connection with the nucleus may, it is supposed, grow again and serve to form another red corpuscle, and so on, the newly formed corpuscles passing meanwhile into the circulation.

It must be added that Rindfleisch has not actually observed the separation of the two parts of the corpuscle; and that the opinion he expresses that the bicon-

cave form is the result of mechanical impressions upon the cup-shaped corpuscles during their passage through the vessels will not hold good for those red disks which are developed as such in the interior of cells in the manner described in paragraph 1, and is therefore rendered unnecessary in regard to other cases.

4. In the spleen.—It has long been believed that the formation of red blood-corpuscles is carried on in the spleen pulp, but this view has been in many quarters supplanted by the contrary one that a destruction of red corpuscles rather than a new formation may there take place, in support of which many facts were brought forward by Kölliker. The former view has, however, been again brought into prominence by Bizzozero, who describes in the spleen pulp after severe loss of blood, nucleated red corpuscles like those in the marrow, and further finds that there are more red as well as white corpuscles in the blood of the splenic vein than in that of the corresponding artery. The subject is one which needs reinvestigation.

5. From the corpuscles of Zimmermann.—Hayem describes as the precursors of the red blood-corpuscles in mammals the small colourless disks which are found floating freely in the blood, and are known as the elementary particles of Zimmermann. To these he applies the name "hæmatoblasts," and he maintains that they acquire colour, and by a gradual increase in size become directly transformed into red corpuscles. In support of this view he asserts that red corpuscles which are much smaller than the ordinary ones are to be almost always met with in blood, and that these smaller forms are especially numerous in cases where there has been previously a considerable loss of blood, and in which, therefore, it may well be supposed that a new formation of red corpuscles is proceeding; and further that they present every transition between the corpuscles of Zimmermann and the red disks.* In the frog Hayem describes as hæmatoblasts, spindle-shaped cells something like the white corpuscles, but of more delicate appearance (like the corpuscle marked *p* in fig. 27). These become, according to him, converted directly into red corpuscles, after undergoing an increase of size and a change of shape, in addition to the accession of colouring matter. They had been long previously noticed by Recklinghausen, and regarded as transition forms between the white and red corpuscles.

Historical.—The development of blood-corpuscles in isolated patches in the vascular area of the chick was first recognised by Pander, who termed the patches "blood-islands." Remak, and after him, His and Kölliker described the first vessels in the vascular area of the chick as originating in the form of a solid cord of mesodermic cells, arranged so as to form a network; the peripheral cells of the vascular cords becoming flattened and forming the epithelium of the vessels, whilst the centrally placed cells become directly converted into blood-corpuscles, acquiring colour first of all at certain points—the blood-islands of Pander—and fluid accumulating between them to form the liquor sanguinis. His stated, moreover, that the blood-vessels within the body of the embryo originate as ingrowths from these vessels of the vascular area. Stricker was the first to describe the formation of blood-vessels by the hollowing out of connective tissue cells, and Afanasieff and Klein proved that the blood-islands of Pander were cells of the mesoderm, in the interior of which blood-corpuscles had made their appearance, and that the containing cells became the first blood-vessels. Klein's account was confirmed, and in some particulars modified by Balfour. The account above given of the formation of vessels and blood-corpuscles in the vascular area of mammals is derived from original observations upon the embryo of the guinea-pig, which have not previously been published *in extenso*. The production of red blood-disks in the interior of cells of the connective tissue was first noticed by me in the subcutaneous connective tissue of the new-born rat, and subsequently in the embryos of a number of different animals, and these observations have been confirmed by Ranvier—who terms the connective tissue cells concerned in the process "vasoformative cells"—as well as by Leboucq and others. It is probable

* A similar account of the development of the red disks was given by Zimmermann; but many of the transitional forms which he described were red corpuscles which had been decolourised by the action of water.

that various appearances which have been described and differently interpreted —*e.g.*, the protoplasmic masses filled with blood-corpuscles noticed by Neumann in the embryonic liver—relate to the same phenomenon.

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EPITHELIAL TISSUE.

General nature and situation.—It is well known, that when the skin is blistered, a thin, and nearly transparent membrane, named the cuticle or epidermis, is raised from its surface. In like manner a transparent film may be raised from the lining membrane of the mouth, similar in nature to the epidermis, although it has in this situation received the name of "epithelium;" and under the latter appellation, a coating of the same kind exists on nearly all free surfaces and membranes of the body.

The following are the most important situations in which a covering or lining of epithelial tissue is found: viz., 1. On the surface of the skin. 2. On mucous membranes; a class of membranes to be afterwards

described, which line those internal cavities and passages of the body that open exteriorly,—viz., the alimentary canal, the lachrymal, nasal, tympanic, respiratory, urinary, and genital passages; as well as the various glandular recesses and ducts of glands, which open into these passages or upon the surface of the skin. 3. On the inner or free surface of serous membranes, which line the walls of closed cavities in the chest, abdomen, and other parts. 4. On the inner surface of the heart, blood-vessels and lymphatics.

In many parts of the connective tissue the cells of that tissue are flattened out and arranged close together, edge to edge, in such a manner as to form a membrane of cells, which so far would come under the definition of the term epithelium. But the cells in question exhibit every transition to the other cells of the connective tissue, so that the enumeration of them under epithelium would create an artificial separation between cells of the same elementary tissue. They may, however, be conveniently described as epithelium-like or epithelioid. Many histologists are of opinion that a similar distinction should be made for the epithelium of the serous membranes and of the vessels, because these are developed in the mesoderm and in connective tissue, and it is the following up of this idea which has led to the wide-spread adoption of the etymologically incorrect word "endothelium" to express an epithelium so derived.* But, if every epithelium which originates in the mesoderm is to be separated, we shall be compelled to separate from the other epithelial tissues, with which they are in every way closely allied, the epithelia of the renal, and of the generative organs, since these are derived from a part of the same layer of cells as gives origin to the epithelium of the serous membranes. And indeed, since it has been shown in more than one instance amongst invertebrates, and in one vertebrate (Amphioxus), that the epithelium of the serous cavities, and even that of the vascular system, is directly derived from an undoubtedly epithelial layer—namely, the entoderm—it is not improbable that this may be the original and typical mode of origin of the so-called endothelia, although it may have become obscured in the more complicated course of development of higher vertebrates. And if this is the case, there is still less reason to regard "endothelium" as a distinct variety of tissue, and to separate it from the epithelial tissues with which it has so long been classed.

Structure of Epithelial Tissue in general.—Every epithelial tissue is formed entirely of cells united together by cohesive matter, which is often in too small quantity to be apparent. The layer or layers thus formed take the shape of the surface to which they are applied, following accurately all its eminences and depressions. No blood-vessels penetrate into epithelial tissue, although in some cases minute channels may exist between the cells into which the plasma of the blood derived from the blood-vessels of the subjacent connective tissue may pass for the nutrition of the epithelium cells.

Nerves are abundant in many epithelia, the nervous fibrils passing in the form of fine varicose filaments among the epithelium cells.

* The term "epithelia," which has passed into "epithelium," was introduced by Ruysch to designate the cuticular covering on the red part of the lips. The word "epidermis" he considered inappropriate, as the subjacent surface is not skin (*derma*); but, as it is beset with papillæ, he named the covering layer "epi-thelia," from ἐπι and θηλη, a nipple or papilla. The use of the term has, by a not unusual license, been extended so as to signify the same kind of coating when it spreads over non-papillary surfaces. The word "endothelium," recently applied by some German writers to distinguish what has heretofore been spoken of as the epithelium lining the serous membranes, and the inner surface of blood-vessels and lymphatics, appears to me a needless innovation, and, considering the literal meaning of the word, not a happy one.—Note by Dr. Sharpey.

In certain situations branched connective tissue cells which may contain pigment lie in the intercellular substance, whilst "migratory cells" are of frequent occurrence between the cells of an epithelium.

Epithelium cells vary in structure as well as in shape, and some of these differences will be mentioned in speaking of the varieties of epithelium. The nucleus varies, however, far less than the rest of the cell: in most cases it has an intranuclear network and one or more nucleoli. In the division of epithelium cells, it undergoes the changes which have already been described.

According to Klein's observations the protoplasm of all kinds of epithelium-cells is a fine reticulum, and this reticulum is in continuity with the intra-nuclear network. This is illustrated in the four cells shown in the accompanying figure (fig. 38).

Fig. 38

Fig. 38.—Structure of different epithelium cells according to Klein.

1, an ordinary epithelium cell; 2, a ciliated cell; 3, a columnar cell; 4, a mucous "goblet" cell.

Classification of Epithelia.—The varieties of epithelium may be classified in various ways, but none perhaps are altogether satisfactory. Thus we may distinguish an epithelium according to its origin, as ectodermic, mesodermic, or entodermic, and this distinction is partially indicated when a separate term (endothelium) is used to denote mesodermic epithelium. Or again, the epithelia may be classed according to their function, and in this way we distinguish between the protective, the secreting, the ciliated, and the sense epithelia. But without failing to recognize that these modes of classification have a certain amount of importance, it will be most convenient here to follow the prevalent custom, and to classify the varieties of epithelium cells according to their shape and arrangement.

In the first place we may distinguish an epithelium which is composed of only a single layer of cells as a *simple* epithelium in contra-distinction to a *stratified* epithelium, in which the layers of cells are numerous. Where, on the other hand, the cells are in more than a single layer, but the two or three layers dove-tail the one into the other, so that the structure is not distinctly stratified, the term *transitional* may be employed; since this kind of arrangement is often found in places

where a simple epithelium passes gradually into one of the stratified variety.

Simple Epithelia.—1. Pavement. Amongst the simple epithelia the most common variety is the *tesselated* or *pavement*, or as it is sometimes named, the simple scaly epithelium. In this the cells form polygonal plates or scales,

Fig. 39.

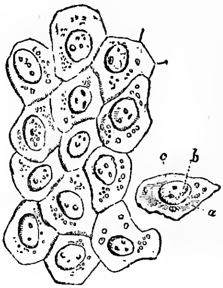

Fig. 39.—Pavement epithelium from a serous membrane (peritoneum); magnified 410 diameters.

a, cell-body; *b*, nucleus; *c*, nucleoli (Henle).

which fit together by their edges like the tiles of a mosaic pavement. The lines of junction of the cells may be straight, or they may be more or less jagged or sinuous. The mesodermic epithelia, such as the epithelium of serous membranes and of the vessels, belong, for the most part, to this variety, but it includes also the epithelium lining the alveoli of the lungs which is of entodermic origin; that covering the outer surface of the membrana tympani, and that lining the mammary ducts, both of which are ectodermic.

2. Columnar. A second variety of simple epithelium is the *columnar*, or *cylinder* epithelium, in which the cells have a prismatic figure, and are set upright on the surface which they cover. In profile a row of these cells looks for the most part like a close palisade (fig. 41); but viewed

Fig. 40.

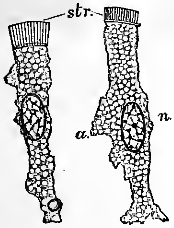

Fig. 41.

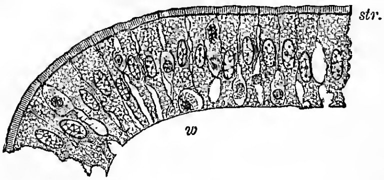

Fig. 40.—Columnar epithelium cells of the rabbit's intestine (E. A. S.).

The cells have been isolated after maceration in very weak chromic acid. They are much vacuolated, and one of them (2) has a fat-globule near its attached end; the striated border (*str.*) is well seen, and the bright disk separating this from the cell-protoplasm; *n*, nucleus with intranuclear network; *a*, a thinned out wing-like projection of the cell which probably fitted between two adjacent cells.

Fig. 41.—A row of columnar cells from an intestinal villus of the rabbit (E. A. S.).

str, striated border; *w*, smaller cells between the epithelium cells, probably of the nature of pale blood- or lymph-corpuscles.

from the surface each cell has a polygonal outline, the cells being flattened where they touch, from mutual compression, so that thus again a mosaic pattern is produced. Columnar epithelium cells vary much in form, in dimensions, and even in structure. Those which may be looked upon as typical are of a long tapering figure, the finer extremity being set upon a surface, and the other and larger end being free. At their sides and edges the columnar cells are often irregular

and jagged, especially where, as is often the case, small lymphoid or other cells are met with between the epithelium cells (fig. 41, *w*). Indeed the cells are not by any means so regular in shape as they are often figured, being often compressed laterally, and sometimes extended sideways into flattened lamellæ (fig. 40, *a*), which fit between the adjacent cells of the epithelium. There is always a distinct oval nucleus which contains an intranuclear network. The nucleus may cause a bulging in the part of the cell in which it is situated, and the nuclei of adjacent cells are on this account often seated in different planes. The protoplasm of the cell usually appears granular, but on closer inspection with higher powers it may be seen that the granular appearance is caused by the existence of vacuoles in it, which may be so numerous as to give the protoplasm which encloses them a reticulated aspect (see p. 4). The cell may contain fatty globules and other substances, among which the most deserving of mention is mucin, the chief organic constituent of mucus. The mucin is apt to distend those cells in which it is contained, especially the part nearest the free border; on contact with any watery fluid the mucus swells and escapes; while at the same time the nucleus is often pressed down towards the finer extremity. Columnar epithelium cells which are thus altered by distension of the outer or free part of the cell by mucus are termed from their shape "goblet or chalice cells" (fig. 42).

Fig. 42.

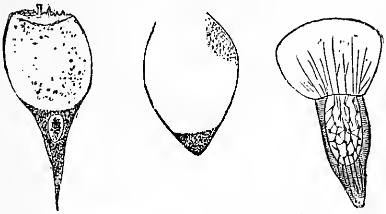

Fig. 42.—Goblet-cells. highly magnified (Klein).

The right-hand cell shows distinctly the intranuclear network, as well as an appearance of fine filaments both in the lower part of the cell and radiating into the swollen, mucus-containing free part.

But typical columnar epithelium cells have another peculiarity. The free border differs from the rest of the cell in being much more highly refracting and finely striated. This striated border of the cell (figs. 40 and 41, *str.*) is commonly termed the cuticular layer, and it is thereby assumed that it is composed of something different from the cell-protoplasm. It does not, however, appear to offer a greater resistance to the action of reagents, for those which destroy the protoplasm of the cell destroy also the striated border. After having been hardened by reagents it may be detached from the rest of the cell, and since the striated free borders of adjacent cells often adhere together, a continuous membrane may thus be obtained, marked by fine lines indicating the division between the cells from which this "cuticula" has become detached. The fine striæ may either represent minute pores in the membrane, as supposed by Kölliker and Funke, or they may be caused by the existence of solid rods or columns composing it, as maintained by Brettauer and Steinach, as well as by Henle. In some cells it may be seen that the striated cuticula is not immediately in contact with the protoplasm of the cell, but is separated from it by a thin disk composed of a substance which refracts the light even more than the striated border. This disk (shown in fig. 40) corresponds

in situation to the bright border of the ciliated epithelium cells (see below), and it is possible that the striated border is the morphological equivalent of the bunch of cilia upon those cells. Columnar epithelium cells are met with in their most characteristic form lining the mucous membrane of the intestines.

Some columnar epithelium cells are very long, others very short, so as to look cubical when seen in profile. They vary in form, moreover, according to the shape of the surface which they cover, thus they may be larger at the base than at the free end, as when they line a tube or duct, and in a section of this they then appear wedge-shaped.

Fig. 43.

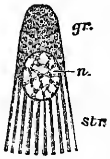

Fig. 43.—Striated epithelium cell, from the duct of a salivary gland (E. A. S.). Highly magnified.

gr, granular protoplasm; *str*, striated protoplasm; *n*, nucleus.

Some epithelium cells, which must be reckoned in with this variety, have a peculiar striated aspect in the basal or fixed half of the cell (fig. 43, *str.*). This is the case with the cells which line the smaller ducts of the salivary glands and some of the tubules of the kidney.

In the human subject, columnar epithelium is chiefly but by no means exclusively derived from the entoderm.

3. Spheroidal or glandular Epithelium.—The cells composing a simple epithelium, are in some cases solid and rounded or polyhedral in shape, no one dimension especially predominating. This variety of epithelium is named *spheroidal*, or since it is chiefly characteristic of the terminal recesses or alveoli of secreting glands, it is often known as *glandular*. The protoplasm of the cells is generally occupied by the materials which the gland secretes.

Fig. 44.

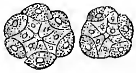

Fig. 44.—Transverse section of two glands of the stomach showing the ovoidal and polyhedral secreting cells (Heidenhain).

Fig. 45.

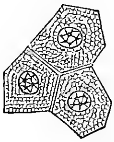

Fig. 45.—Three polyhedral epithelium cells from the liver of the guinea-pig (Klein).

The protoplasm of the cells has a reticular aspect.

4. Ciliated Epithelium.—Lastly the cells of a simple epithelium may bear on their basal or free ends spontaneously moving filaments named *cilia*. In the human subject the ciliated epithelium is not always perfectly simple, for there are often other non-ciliated cells placed between the attached ends of those which bear the cilia. The ciliated epithelium will be best considered as a whole after the remaining varieties of epithelium have been touched upon.

Fig. 46.

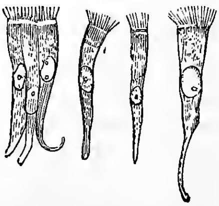

Fig. 46.—Columnar ciliated epithelium cells from the human nasal membrane; magnified 300 diameters (Sharpey).

Stratified Epithelium.—In a stratified epithelium the cells, as we have seen, are disposed in a number of layers, and it is commonly found that the cells of these various layers exhibit every variety of shape. As

Fig. 47.

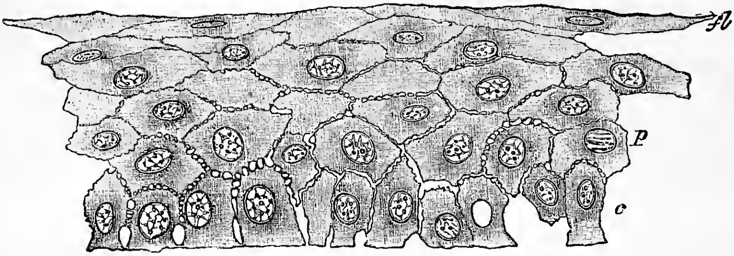

Fig. 47.—Section of the stratified epithelium covering the front of the cornea of the eye. Highly magnified. (E. A. S.)

c, lowermost columnar cells; *p*, polygonal cells above these; *fl*, flattened cells near the surface. The intercellular channels, bridged by minute processes of the cell, are well seen. The lower part of the section on the right is somewhat broken.

a rule the cells of the deepest or attached layer are columnar (fig. 47, *c*), and the superficial cells are flattened scales (fig. 47, *fl*) which may be of considerable size, but which do not, like the cells of pavement or simple scaly epithelium, fit together by their edges, but, on the contrary, overlap one another (fig. 48). The cells of the layers immediately external to the columnar layer are rounded in shape, or at least only so far modified as to enable them to fit to the columnar cells and to one another (fig. 47, *p*); but as we trace the strata towards the surface, we find the component cells becoming more flattened and larger, whilst at the same time undergoing a change in their chemical constitution, so that at first the external part, and afterwards the whole of the protoplasm of the cell, is converted into horny substance, even the nucleus being at last involved.

Fig. 48.

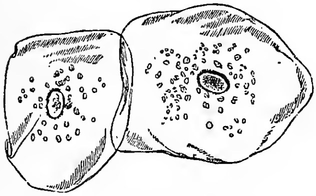

Fig. 48.—Epithelium-scales from the inside of the mouth; magnified 260 diameters (Henle).

The deeper protoplasmic cells of a stratified epithelium are continually multiplying by cell-division, and, as the new cells which are thus produced in the deeper parts increase in size, they compress and push outwards those previously formed. In this way cells which were at first deeply seated, become gradually shifted towards the surface, undergoing meanwhile the chemical change above spoken of. The older superficial cells are continually being removed by attrition and abrasion, while others rise up to supply their place.

The deeper layers of a stratified epithelium are not closely applied to one another by their edges, but there exists a system of intercellular

channels, which are bridged across by spikes and ridges, which project from the surfaces of the cells and abut against the corresponding spikes and ridges on the surfaces of the adjoining cells (see fig. 47). When the cells are isolated, the spikes and ridges can be better seen (fig. 49), especially if the intercellular channels have become widened in consequence of an excess of fluid accumulating in them, as may happen under certain pathological conditions.

Fig. 49.

Fig. 49.—Two "PRICKLE-CELLS" FROM THE DEEPER PART OF THE EPIDERMIS (Ranvier).

d, space around the nucleus, probably caused by shrinking of the latter.

The spikes and ridges upon the deeper cells of a stratified epithelium were first noticed by Max Schultze, who was of opinion that they were for the purpose of effecting, by indenting with those on adjoining cells, a firmer connexion between the cells of the epithelium. The true relations of the structures in question, and the intercellular channels which are bridged across by them, were discovered by Bizzozero. The researches of J. Arnold and of Thoma have shown that similar channels occur extensively in all varieties of epithelium.

Stratified scaly epithelium occurs in one of its simplest and most typical forms covering the anterior surface of the cornea of the eye (fig. 47). It is found also lining the mouth, the chief part of the pharynx, and the œsophagus, and in the female it lines the vagina and part of the cervix uteri, but its most extensive distribution is over the surface of the skin, where it forms the epidermis. In many parts of this the layers become very numerous, and their arrangement somewhat complicated, as will be noticed in the description of the skin. It may be remarked that, in most of the situations where it is found, stratified scaly epithelium is of ectodermic origin.

Transitional Epithelium.—Epithelium to which the term transitional may be applied, as being in a sense intermediate between those forms which consist of but a single layer of cells and the stratified which we have just described, may be classed under the three heads of columnar, ciliated, and scaly transitional, according to the kind of cell in each which happens to be most prominent or superficial. The columnar and ciliated transitional epithelia differ, however, so very slightly from the corresponding simple epithelia—viz., merely in the presence between the fixed ends of the columnar and ciliated cells of smaller and probably younger epithelium cells irregularly disposed—that they do not seem to merit any special description. But the scaly transitional epithelium which is met with lining the urinary bladder and ureters presents several peculiarities. It consists of three or four layers of cells, of which the inner or most superficial are large flattened scales when examined from the distended bladder (fig. 51, *a*); almost cubical in shape when taken from the collapsed organ; smooth over their free surface, but pitted on the opposite side, being moulded over the rounded ends of the cells which form the next layer. These are pyriform, and the smaller end of the pear is set upon the subjacent connective tissue, whilst the larger end has the position just mentioned (fig. 51, *b*, *c*). Filling up the intervals between these tapering cells are the smaller

irregular cells of the third layer. All these cells have distinct nuclei, and in the flattened superficial cells two nuclei may often be seen in the cell. If this, as probably is the case, is an indication that the cell is

Fig. 50.

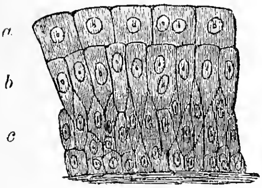

Fig. 51.

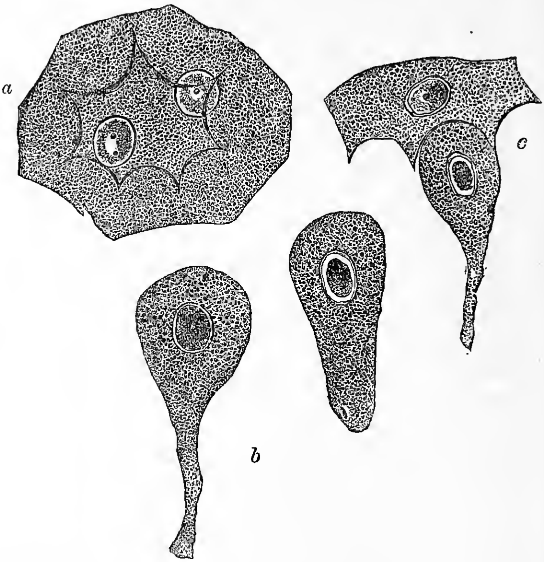

Fig. 50.—Section of the epithelial lining of the ureter; man (Kölliker).
a, superficial; *b*, intermediate; and *c*, deep layer of cells.

Fig. 51.—Epithelial cells from the bladder of the rabbit. Highly magnified. (Klein.)

a, large flattened cell from the superficial layer, with two nuclei, and with strongly marked ridges and intervening depressions on its under surface; *b*, pyriform cells of the second layer; *c*, pear-shaped cell of the second layer showing the manner in which it is adapted to a depression on the superficial cell.

about to divide, the mode of growth of this kind of epithelium must be different from that of the stratified scaly variety, in which the multiplication of the cells appears to take place exclusively in the deeper layers.

CILIATED EPITHELIUM.

In this form of epithelium, the cells which are generally columnar, bear at their free extremities little hair-like processes, which are agitated incessantly during life, and for some time after systemic death, with a lashing or vibrating motion. These minute and delicate moving organs are named *cilia*. They exist very extensively throughout the animal kingdom; and the movements which they produce are subservient to very varied purposes in the animal economy.

Distribution and use.—In the human body ciliated epithelium occurs in the following parts, viz:—1. On the mucous membrane of the air passages and its prolongations. It commences at a little distance within the nostrils, covers the membrane of the nose (except the proper olfactory part) and of the adjoining bony sinuses, and extends up into

the nasal duct and lachrymal sac. From the nose it spreads backwards a certain way on the upper surface of the soft palate, and over the upper or nasal region of the pharynx; thence along the Eustachian tube and lining membrane of the tympanum, of which it covers the greater part. The lower part of the pharynx is covered by scaly epithelium as already mentioned; but the ciliated epithelium begins again in the larynx a little above the glottis, and continues throughout the trachea and the bronchial tubes in the lungs to their smallest ramifications. Over the vocal cords, however, the epithelium is of the stratified scaly variety. 2. On the mucous lining and in the glands of the uterus, commencing at the middle of the cervix and extending along the Fallopian tubes, even to the peritoneal surface of the latter at their fimbriated extremities. 3. Lining the *vasa efferentia, coni vasculosi*, and first part of the excretory duct of the testicle. 4. To some extent on the parietes of the ventricles of the brain, and throughout the central canal of the spinal cord. 5. In the excretory ducts of certain small racemose glands of various parts (tongue, pharynx, &c.). 6. In the embryo, lining the œsophagus and parts of the stomach and extending also over the whole of the pharynx.

In other mammiferous animals, as far as examined, cilia have been found in nearly the same parts.* To see them in motion, a portion of epithelium may be scraped off from any ciliated mucous membrane and examined in a drop of weak solution of salt (·75 per cent.) or serum of blood. When it is now viewed with a magnifying power of 200 diameters or upwards, a very obvious agitation will be perceived at the edge of the detached piece of epithelium; this appearance is caused by the moving cilia, with which the surface of the membrane is covered. Being set close together, and moving simultaneously or in quick succession, the cilia, when in brisk action, give rise to the appearance of a bright transparent fringe along the margin of the membrane, agitated by such a rapid and incessant motion, that the single threads which compose it cannot be perceived. The motion here meant, is that of the cilia themselves; but they also set in motion the adjoining fluid, driving it along the ciliated surface, as is indicated by the agitation of any little particles that may accidentally float in it. The fact of the conveyance of fluids and other matters along the ciliated surface, as well as the direction in which they are impelled, may also be made manifest by immersing the membrane in fluid, and dropping on it some finely-pulverised substance (such as charcoal in fine powder), which will be slowly but steadily carried along in a constant and determinate direction; and this may be seen with the naked eye, or with the aid of a lens of low power. (Sharpey.)

The ciliary motion of the human mucous membrane is well seen on the surface of recently-extracted nasal polypi; and single ciliated particles, with their cilia still in motion, are sometimes separated accidentally from mucous surfaces in the living body, and may be discovered in the discharged mucus; or they may even be purposely detached by gentle abrasion.

Cilia have been shown to exist in almost every class of animals, from the highest to the lowest.† The immediate purpose which they serve is,

* Cilia have also been seen in some mammals at the commencement of the tubules of the kidney (Klein), a situation where in lower vertebrates they have long been known to exist.

† The Crustacea offer a singular exception, and it is remarkable that in most of them the spermatozoa are also devoid of a vibratile filament.

to impel matter, generally more or less fluid, along the surfaces on which they are attached; or, to propel through a liquid medium the ciliated bodies of minute animals, or other small objects which are provided with cilia; as is the case with many infusorial animalcules, in which the cilia serve as organs of locomotion like the fins of larger aquatic animals. In many of the lower tribes of aquatic animals, the cilia acquire a high degree of importance: producing the flow of water over the surface of their organs of respiration, indispensable to the exercise of that function; enabling the animals to seize their prey, or swallow their food, and performing various other offices of greater or less importance in their economy. In man and the warm-blooded animals, their use is apparently to impel secreted fluids or other matters along the ciliated surface, as, for example, the mucus of the windpipe and nasal sinuses, which they carry towards the outlet of these cavities.

Structure.—The cells of the ciliated epithelium (fig. 52) contain oval nuclei, exhibiting for the most part a distinct intra-nuclear network,

Fig. 52.

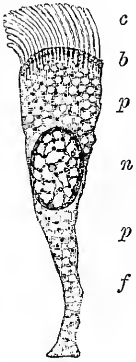

Fig. 53.

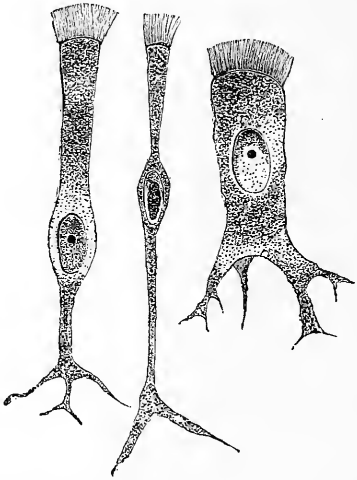

Fig. 52.—A ciliated epithelium-cell from the trachea of the rabbit, isolated in very weak chromic acid; highly magnified (E. A. S.).

p, *p*, protoplasm of the cell, filled with clear vacuoles; *n*, nucleus, showing nuclear membrane, nucleoplasmic network, and nucleolus; *c*, fringe of cilia; *b*, bright border of the cell through which the cilia pass; *f*, fixed end of the cell.

Fig. 53.—Ciliated epithelium cells from the trachea of the cat (Klein).

The fixed ends of the cells are irregularly forked.

and one or more bright nucleoli. Viewed with a moderate magnifying power, their protoplasm looks granular, but with a high power it is seen to be finely vacuolated, although the free border of the cell through which the cilia pass presents a clear aspect (fig. 46). The cells have most generally an elongated form, like the particles of the columnar epithelium, which they resemble too in arrangement, but they are often of greater length and more pointed at their lower end; and this is not unfrequently irregularly forked in those parts where a deeper layer of cells exists below the

ciliated cells (fig. 53). The cilia are attached to their broad or superficial end, each cell bearing a tuft of these minute hair-like processes. In some cases, the cells are shorter and cubical in figure, and when completely detached may appear spheroidal, as shown in fig. 54, which represents such cells from the epithelium of the frog's mouth. In man this form occurs in the ciliated epithelium of the cerebral ventricles and that of the tympanum, where the cells form but a single stratum. The columnar ciliated epithelium may exist as a simple layer, as in the uterus and Fallopian tubes, the finest ramifications of the bronchia, and the central canal of the spinal cord: but in various other parts—as the nose, pharynx, Eustachian tube, the trachea and its larger divisions—there is a layer of elongated and irregular cells beneath the superficial ciliated range, filling up the spaces between the pointed and forked extremities of the latter. Probably the subjacent cells acquire cilia, and take the place of ciliated cells, which are cast off; but the mode of renovation of ciliated epithelium is not yet fully understood.

Fig. 54.

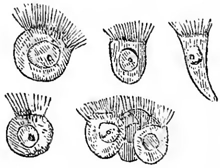

Fig. 54.—Ciliated cells from the mouth of the frog; magnified 300 diameters (Sharpey).

It is stated that when the ciliated epithelium is artificially removed from a portion of the inner surface of the rabbit's trachea, the denuded surface speedily becomes again covered with epithelium, which grows over it from the edge, but the cells form at first a single layer of flattened epithelium. They next acquire cilia, and afterwards become columnar, the epithelium thus assuming the character which it has normally in that situation.

There is no reason to believe that the ciliated epithelium cells are in connection either with nerve fibres, or with the cells of the subjacent connective tissue. It is true that such anatomical connection has been described by Lockhart Clarke and Gerlach in reference to the columnar ciliated epithelium of the central canal of the spinal cord and of the Sylvian aqueduct. But this is a most difficult point to determine exactly, and even if such a connection should be proved, the cells in the situations above mentioned are entirely different in many respects from ordinary ciliated cells. They are relatively slender, and their fixed non-ciliated ends pass into fine branching fibres, which lose themselves in a fibrillar network which underlies the epithelium, and appears to be formed chiefly, if not entirely, by the interlacement of the ramified cell-processes. These peculiar ciliated cells closely resemble those which constitute the structures known as nerve-epithelia in some of the lower invertebrata, and which in some of these represent the whole central nervous system.

Size, form and action of the cilia.—The cilia themselves differ widely in size in different animals, nor are they of equal size in all parts of the same animal. In the human windpipe they measure $\frac{1}{4000}$th to $\frac{1}{2500}$th of an inch in length; but in many invertebrate animals they are much larger than this, and in the human epididymis are from eight to ten times longer than in the trachea.

In figure they have the aspect of slender conical, or slightly flattened filaments; broader at the base, and usually pointed or rounded at their free extremity. Their substance is transparent, soft and flexible. It is to all appearance homogeneous, and no fibres, granules, or other indications of definite internal structure, have been satisfactorily demonstrated in it. According to Engelmann, cilia are doubly refracting; but this character is by no means very obvious.

In all probability the substance composing the cilia is chemically and otherwise similar to the cell-protoplasm, of which they seem to be permanent protrusions.* If this is the case, there is no difficulty in supposing that the lashing, whip-like movement of each cilium is effected by the contractility of the cilium itself, this being, however, called into action by a stimulus originating in the protoplasm of the cell to which it is attached. For if the cilia be detached they cease to move, although the isolation of the ciliated cell from its neighbours and from the other tissues does not cause a cessation of the movement. On this account it is thought, by some, that the movement is entirely a passive one, caused by the contraction of the cell-protoplasm acting upon the base of the cilium, and if this were so, there would be no need to assume that the cilia are themselves contractile. But the apparently inherent motion of the tails of the spermatozoa, which are comparable to long single cilia, and that of the long cilia which are protruded from many of the lower animal and plant organisms, seem to indicate that the movement is inherent in the cilia themselves. The cilia vibrate with a frequency of not less than ten times in a second when moving actively, but the rate of movement may be much slower than this. The movement of cilia is incessant so long as the cells remain alive, but that of spermatozoa often exhibits intervals of rest alternating with periods of rhythmic movement.

The manner in which the cilia move, is best seen when they are not acting very briskly. The motion of an individual cilium may be compared to that of a carter's whip, the cilium being rapidly flexed in one direction, that of the current, and returning more slowly to what may be regarded as the position of rest, generally a little on the other side of a plane perpendicular to the surface of the cell. The motion does not involve the whole ciliated surface at the same moment, but is performed by the cilia in regular succession, giving rise to the appearance of a series of waves travelling along the surface, like the waves caused by the wind in a field of corn. When they are in very rapid action the undulation is less obvious, and, as Henle remarks, their motion then conveys the idea of swiftly-running water. The undulating movement may be beautifully seen on the gills of a mussel. The undulations, with some exceptions, seem always to travel in the same direction on the same parts. The impulsion, also, which the cilia communicate to the fluids or other matters in contact with them, maintains a constant direction; unless in certain of the lower animals, in which the motion is often variable and arbitrary in direction, and might even be supposed to be voluntary. Thus in the windpipe of mammalia, the mucus is conveyed upwards towards the larynx, and, if a portion of the membrane be detached, matters will still be conveyed along the surface of the separated fragment in the same direction relatively to that surface, as before its separation.

The persistence of the ciliary motion for some time after death, and the regularity with which it goes on in parts separated from the rest of the body, sufficiently prove that, with the possible exceptions alluded to, it is not under the influence of the will of the animal, nor dependent for its production on the nervous centres, and it does not appear to be influenced in any way by stimulation or sudden destruction of these centres. The time during which it continues after death or separation differs in different kinds of animals, and is also materially influenced by

* According to Klein they are in continuity with the intracellular network (see fig. 38, 2.)

temperature and by the nature of the fluid in contact with the surface. In warm-blooded animals the period varies from two or three hours to two days, or even more; being longer in summer than in the cold of winter. In frogs the motion may continue four or five days after destruction of the brain and spinal cord; and it has been seen in the gullet of the tortoise fifteen days after decapitation, continuing seven days after the muscles had ceased to be irritable.

Effect of varying external conditions and reagents upon ciliary motion. —Variations of temperature exert a very marked effect upon the rate and vigour of the motion of cilia. Thus, in warm-blooded animals it is altogether stopped if the temperature is lowered to 6° C., whereas, in cold-blooded animals, such as the frog and mussel, it goes on unimpaired at 0° C. The motion which has become quiescent from cold, may be revived by warmth, and becomes more active in proportion to the rise in temperature up to a certain point, which differs in warm and cold-blooded animals. In the former, this maximum temperature is about 45° C.; above this the movement quickly ceases, the cilia passing into a coagulated stiffened condition, known as heat-rigor, and which, if well marked, is not recovered from. The temperature of the body seems to be that which is most favourable to the action of the cilia; that is to say, they will, if removed from the body, work vigorously for a longer time at this temperature than at any other.

Cilia will continue to work for a time in the absence of free oxygen. This was shown by Sharpey, who noticed the movement of the cilia upon the gill of the tadpole to proceed for some hours, even when immersed in water which had been deprived of its oxygen by boiling. This experiment shows that like the substance of muscle, the protoplasm of the ciliated epithelium-cell can store up oxygen in a combined form for future use.

The immediate action of water is to increase the activity of cilia, and this is accompanied by a swelling of the cilia through imbibition of fluid. Agents or conditions, on the other hand, which abstract water from the tissue, retard or arrest the action. Thus most of the common acid and saline solutions when concentrated arrest the action of cilia instantaneously in all animals, but dilution delays this effect, and when carried far enough, prevents it altogether. Fresh water soon arrests the motion in marine animals; but it evidently acts by destroying both the form and substance of the cilia, which in these cases are adapted to a different medium. Even in air-breathing and fresh-water animals fresh water has after a time the same action, provided the ciliated cells are detached, so that it can pass by imbibition into their protoplasm. Solutions of potash or soda, if extremely dilute, act like water, but more powerfully. Virchow observed that a solution of either potash or soda would even revive the movement of cilia after it had just ceased. Narcotic substances, such as hydrocyanic acid, salts of morphia and strychnia, opium and belladonna, were stated by Purkinje and Valentin to have no effect, but the first-named agent appeared to Sharpey to arrest the motion in the river-mussel. The vapour of chloroform arrests ciliary action, but the motion revives again if the application of the vapour is discontinued (Lister).

Carbonic acid gas resembles chloroform in its action, rapidly arresting the movement if conveyed over a ciliated surface, but the action speedily recommences on again admitting air. The passage of the gas is, however, generally found to stimulate the movement at first.

Bile stops the action of cilia, while blood prolongs it in vertebrated animals; but the blood or serum of the vertebrata has quite an opposite effect on the cilia of invertebrate animals, arresting their motion almost instantaneously.

It was noticed by Steinbuch that a mechanical stimulus, insufficient to injure the cilia, such as that produced by the impulse of a current of fluid, acts markedly in exciting the activity of ciliary motion.

Electric shocks, unless they cause injury to the ciliated surface (which is sometimes the case), produce no visible effect; and the same is true of galvanic currents. Engelmann states, however, that if the ciliary action be very rapid it may be slowed, if slow it may be accelerated by electricity.

Whatever views are entertained concerning the nature and source of the power by which the cilia act, it must be borne in mind that each ciliated cell is individually endowed with the faculty of producing motion, and that it possesses in itself whatever organic apparatus and whatever physical or vital property may be necessary for that end; for single epithelium cells are seen to exhibit the phenomenon long after they have been completely isolated.

It seems not unreasonable to consider the ciliary motion as a manifestation of that property on which the more conspicuous motions of animals are known to depend, namely, vital contractility; and this view has at least the advantage of referring the phenomenon to the operation of a vital property already recognised as a source of moving power in the animal body. But, assuming this view to be sound, so far as regards the nature of the motile power brought into play, it affords no explanation of the cause by which the contractility is excited and the cilia maintained in constant action.

The first comprehensive account of the structure, distribution, and mode of action of cilia was given by Sharpey in the article "Cilia," in Todd and Bowman's Cyclopædia. That article, which appeared in 1835, was the result of much laborious investigation, and still forms the basis of our knowledge on the subject. The present account was written by Sharpey for the fifth edition of this work, and has since needed but little modification. Simultaneously with Sharpey's article a very complete description was also given by Purkinje and Valentin, including an account of the discovery of this phenomenon in mammals, birds, and reptiles, and of the literature up to that time (De phænomeno generali et fundamentali motûs vibratorii continui, 1835).

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THE CONNECTIVE TISSUES.

Three principal modifications or varieties of connective tissue have long been recognised, consisting of the same structural elements: niamely, *white fibres, elastic fibres* and *connective tissue corpuscles;* but n widely different proportions, and thereby exhibiting a difference in their grosser or more obvious characters and physical properties. They are known as the *areolar*, the *fibrous*, and the *elastic* tissues, and will be now severally treated of. Without disregarding the alliance of cartilage and bone to the connective tissues, we shall not include them in the same general description; but there remain certain forms of tissue, occurring locally, or met with as constituents of other textures, which belong to this group, and will be briefly considered in a separate section as subordinate varieties of connective tissue.

Cartilage and bone are usually included in the group of connective tissues, and of right, for they present undoubted points of relationship with these tissues, both in their nature and the general purpose which they serve in the animal frame. Thus, yellow cartilage shows an unmistakable transition to elastic connective tissue, as fibro-cartilage does, even more decidedly, to white fibrous tissue. Moreover, the animal basis of bone agrees entirely in chemical composition, and in many points of structure, with the last-named tissue. But since both cartilage and bone possess easily recognizable histological features, besides well-marked physical and chemical characteristics, it seems more consistent with the purpose of histological description to treat of them as independent tissues.

AREOLAR TISSUE.

Distribution and arrangement.—If we make a cut through the skin and proceed to raise it from the subjacent parts, we observe that it is loosely connected to them by a soft filamentous substance of considerable tenacity and elasticity, and having, when free from fat, a white fleecy aspect; this is the substance known as *areolar tissue.* In like manner the areolar tissue is found underneath the serous and mucous membranes which are spread over various internal surfaces, and serves to attach those membranes to the parts which they line or invest; and as under the skin it is named "subcutaneous," so in the last-mentioned situations it is called "subserous" and "submucous" areolar tissue. But on proceeding further we find this substance lying between the muscles, the blood-vessels, and other deep-seated parts, occupying, in short, the intervals between the different organs of the body where they are not otherwise insulated, and thence named "intermediate;" very generally, also, it becomes more consistent and membranous immediately around these organs, and under the name of the "investing" areolar tissue, affords each of them a special sheath. It thus forms inclosing sheaths for the muscles, the nerves, the blood-vessels and other parts. Whilst the areolar tissue might thus be said in some sense both to connect and to insulate entire organs, it also performs the same office in regard to the finer parts of which these organs are made up; for this end it enters between the fibres of the muscles, uniting them into bundles; it connects the several membranous layers of the hollow viscera, and binds together the lobes and lobules of compound glands; it also accompanies the vessels and nerves within these organs, following their branches nearly to their finest divisions, and affording them support and protection. This portion of the areolar tissue has been named the "penetrating," "constituent," or "parenchymal."

It thus appears that the areolar is one of the most general and most extensively distributed of the tissues. It is, moreover, continuous throughout the body, and from one region it may be traced without interruption into any other, however distant; a fact not without interest in practical medicine, seeing that in this way dropsical waters, air, blood, and urine, effused into the areolar tissues, and even the matter of suppuration, when not confined in an abscess, may spread far from the spot where they were first introduced or deposited.

On stretching out a portion of areolar tissue by drawing gently asunder the parts between which it lies, it presents an appearance to the naked eye of a multitude of fine, soft, and somewhat elastic threads, quite transparent and colourless, like spun glass; these are intermixed with fine transparent films, or delicate membranous laminæ, and both threads and laminæ cross one another irregularly and in all imaginable directions, leaving open interstices or areolæ between them. These meshes are, of course, more apparent when the tissue is thus stretched out; it is plain also that they are not closed cells, as the term "cellular tissue" which was formerly used to denote the areolar tissue, might seem to imply, but merely interspaces, which open freely into one another: many of them are occupied by the fat, which, however, does not lie loose in the areolar spaces, but is enclosed in its own vesicles. A small quantity of colourless transparent fluid of the nature of lymph is also present in the areolar tissue, but, in health, not more than is sufficient to moisten it.

On comparing the areolar tissue of different parts, it is observed in some to be more loose and open in texture, in others more dense and close, according as free movement or firm connection between parts is to be provided for.

FIBROUS TISSUE.

When the fine bundles of connective tissue are disposed for the most part in one or two directions, instead of interlacing in every direction as in the areolar tissue, they confer a distinctly fibrous aspect to the parts which they compose, accompanied by the acquisition of certain properties, which are mainly due to the parallel disposition of the elements of the tissue, and to the preponderance of the white fibres over the elastic (see below). This *fibrous tissue* is met with in the form of ligaments, connecting the bones together at the joints; it also forms the tendons of muscles, into which their fleshy fibres are inserted, and which serve to attach these fibres to the bones. In its investing and protecting character it assumes the membranous form, and constitutes a class of membranes termed "fibrous." Examples of these are seen in the periosteum and perichondrium which cover the bones and cartilages, in the dura mater which lines the skull and protects the brain, and the fibrous layer which strengthens the pericardium, also in the albugineous coat of the testicle, and the sclerotic coat of the eye, which enclose the tender internal parts of these organs. Fibrous membranes, named "aponeuroses" or "fasciæ," are also employed to envelope and bind down the muscles of different regions, of which the great fascia inclosing the muscles of the thigh and leg is a well-known example. The tendons of muscles, too, may assume the expanded form of aponeuroses, as those of the broad muscles of the abdomen, which form strong fibrous layers in the walls of that cavity and add to their strength. It thus appears

that the fibrous tissue presents itself under two principal forms, the *fascicular* and the *membranous*.

The fibrous tissue is white or yellowish white, with a shining, silvery, or nacreous aspect. It is exceedingly strong and tough, yet perfectly pliant; but it is almost devoid of extensibility. By these qualities it is admirably suited to the purposes to which it is applied in the animal frame. By its inextensible character it maintains in apposition the parts which it connects against any severing force short of that sufficient to cause actual rupture, and this is resisted by its great strength, whilst its flexibility permits of easy motion. Accordingly the ligaments and tendons do not sensibly yield to extension in the strongest muscular efforts; and though they sometimes snap asunder, it is well known that bones will break more readily than tendons of equal thickness, and the fibrous membranes are proportionally strong and alike inextensible.

ELASTIC TISSUE.

In other situations in the body a tissue is found which, while allowing a considerable amount of extension, will readily return to its original condition when the extending force is relaxed. This is provided for by the preponderance of elastic fibres in the connective tissue, and these in the most typical examples of the tissue, such as the ligamentum nuchæ of quadrupeds and the ligamenta subflava of the human spine, give it a yellowish colour. The tissue is extensible and elastic in the highest degree, but is not so strong as ordinary fibrous ligament, and it breaks across the direction of its fibres when forcibly stretched.

Examples of the texture on a large scale are seen in the horse, ox, elephant, and other large quadrupeds, in which it forms the great elastic ligament, called *ligamentum nuchæ*, that extends from the spines of the vertebræ to the occiput, and aids in sustaining the head; in the same animals it also forms an elastic subcutaneous fascia, which is spread over the muscles of the abdomen and assists in supporting the contents of that cavity. In the human body it is met with chiefly in the following situations, viz.:—

1. Forming the *ligamenta subflava*, which extend between the arches of adjacent vertebræ; these ligaments, while they permit the bones to be drawn apart in flexion of the body, aid in restoring and maintaining their habitual approximation in the erect posture—so far, therefore, relieving the constant effort of the erector muscles. There is, moreover, an obvious advantage in having an elastic band in this situation, instead of an ordinary ligament, which would be thrown into folds when the bones are approximated. 2. Constituting the chief part of the stylohyoid, thyrohyoid, and cricothyroid ligaments, and those named the vocal cords. Also extending, in form of longitudinal bands, underneath the mucous membrane of the windpipe and its ramifications. 3. Entering, along with other textures, into the formation of the coats of the blood-vessels, especially the arteries, and conferring elasticity on these tubes.

MICROSCOPIC STRUCTURE OF CONNECTIVE TISSUE.

The three kinds of connective tissue, the obvious characters and arrangement of which have just been described, agree closely with one another in elementary structure. They are all composed of a matrix or ground-substance, in which cells are imbedded, and in this ground-

substance and between the cells are fibres of two kinds, the white and elastic. It is the different arrangement of the cells and fibres, as well as the relative proportion of one kind of fibre to the other, that determines the different characters of the varieties of connective tissue above enumerated.

Ground-substance and Fibres of Connective Tissue.—The **ground-substance,** matrix, or intercellular substance of the connective tissue is composed of a soft homogeneous material which occupies the tissue between the cells and cell-groups, and in which, as above stated, the fibrous elements of the tissue are found, it may be in so great a quantity as altogether to obscure the ground-substance in which they lie. It serves thus to unite the fibres, at least the white fibres, into the bundles which they form, penetrating between the individual fibrils of a bundle, and enveloping the latter with a homogeneous sheath often of great tenuity.

Fig. 55.

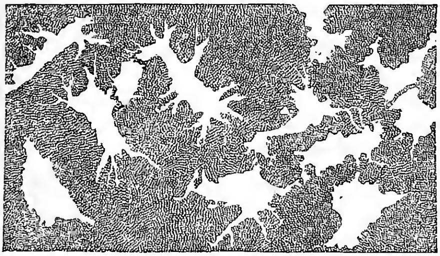

Fig. 55.—Cell-spaces of subcutaneous connective-tissue, the ground substance having been stained deeply by nitrate of silver. (E. A. S.) 340 diameters.

The ground-substance of connective tissue appears to contain mucin. It is precipitated and rendered cloudy by acetic acid. It becomes stained brown when treated with nitrate of silver and afterwards exposed to the light, in this respect resembling the intercellular substance of an epithelium. The cells of the tissue lie imbedded in it, either in shallow pits on the surface, or in spaces—cell-spaces—entirely enclosed by the ground-substance, the spaces being for the most part rather larger than the contained cells, with which, however, they correspond on the whole in shape. These cell-spaces (the Saftkanälchen of Recklinghausen, lymphatic canaliculi of Klein and Burdon-Sanderson) are brought into view when the tissue is stained with nitrate of silver, for they then look white upon the brown ground (figs. 55, 56).

Fig. 56.

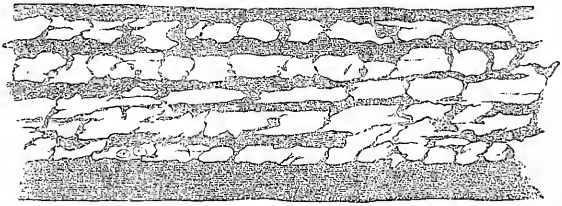

Fig. 56.—Cell-spaces of tendon of mouse's tail, brought into view by treatment with nitrate of silver. 175 diameters. (E. A. S.)

White Fibres.—When examined under the microscope both the areolar and fibrous tissues are seen to be principally made up of exceedingly fine, transparent, and apparently homogeneous filaments, from about $\frac{1}{50000}$ to $\frac{1}{25000}$th of an inch in thickness, or even less (fig. 57). These are seldom single, being mostly united by means of a small and usually imperceptible quantity of the ground-substance into bundles and filamentous laminæ of various sizes, which to the naked eye appear as simple threads and films. Though the bundles may intersect in every direction, the filaments of the same bundle run nearly parallel to each other, and no one filament is ever seen to divide into branches or to unite with another. The associated filaments take an alternate bending or waving course as they proceed along the bundle, but still maintain their general parallelism. This wavy aspect, which is very characteristic of these filaments, disappears on stretching the bundle, but returns again when it is relaxed.

Fig. 57.

Fig. 57.—Filaments of areolar tissue, in larger and smaller bundles, as seen under a magnifying power of 400 diameters Sharpey).

The filaments just described, though transparent when seen with transmitted light under the microscope, appear white when collected in considerable quantity and seen with reflected light ; they are doubly refracting and, therefore, appear bright when viewed between crossed Nichol's prisms. Acetic acid causes them to swell up and become indistinct. When the tissue is boiled in water the white fibres are almost wholly resolved into gelatine ; they are said, therefore, to be composed of collagenous substance.

Elastic Fibres.—Occurring both in the areolar and fibrous tissue, and composing the greater part of the so-called elastic connective tissue, fibres of a different nature from those just considered are found—these are the elastic fibres. When collected in considerable quantity they have, as we have seen, a yellowish colour, but when seen singly their yellow colour does not appear ; they can, however, always be recognised by the following characters. When viewed under a tolerably high magnifying power, they appear quite transparent, with a remarkably well-defined outline (fig. 58). They may run nearly straight, but often follow a somewhat bending course, with bold and wide curves, unlike the undulations of the white connective filaments. As they proceed they divide into branches, and join or anastomose together in a reticular manner (fig. 59). In some parts the elastic networks are composed of fine fibres with wide meshes ; in other parts the elastic fibres are larger and broader and the

intervening spaces narrower, so that the tissue may even have a lamellar character and present the appearance of a homogeneous membrane, which may be either entire, or with gaps or perforations at short intervals, in which case it constitutes the fenestrated membrane of Henle, found in the

Fig. 58.

Fig. 59.

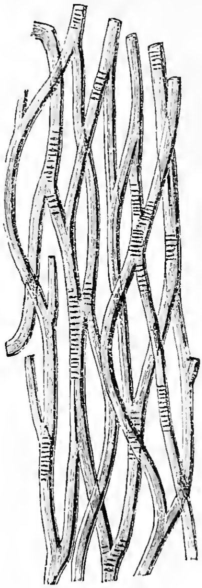

Fig. 58.—Elastic fibres from the ligamenta subflava; magnified about 200 diameters (Sharpey).

Fig. 59.—Elastic fibres from the ligamentum nuchæ of the ox, showing transverse markings on the fibres; highly magnified. (E. A. S.)

coats of the blood-vessels. A remarkable character which elastic fibres exhibit in many specimens, is a tendency to curl up at their broken ends; and these ends are not pointed, but abruptly broken across. Their size is very various; the largest in man are nearly $\frac{1}{4000}$th of an inch in diameter, the smallest perhaps not more than $\frac{1}{24000}$th. In some situations the larger sized fibres prevail; this is the case with the ligamenta subflava, where their general diameter is about $\frac{1}{7500}$th of an inch; in other instances, as in the vocal chords and in many parts of the areolar tissue, the elastic fibres are exceedingly fine. In some animals elastic fibres are met with $\frac{1}{1500}$th of an inch in thickness. In shape they are not cylindrical but angular, as is well seen in transverse section (fig. 60).

Fig. 60.

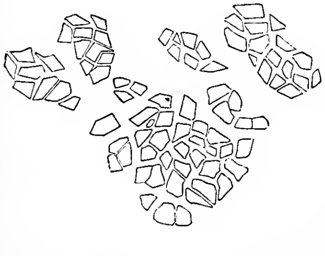

Fig. 60.—Cross-section of elastic fibres from the ligamentum nuchæ of the ox (from a sketch by Mr. T. P. Gostling).

In certain portions of the areolar tissue, as for instance in that which lies under the serous and mucous membranes of particular regions, the yellow or elastic fibres are abundant and large, so that they cannot well be overlooked; but in other parts and in the fibrous tissue, they are few in number, and small, and are then in a great measure hidden by the white filaments; in such cases, however, they can generally be

Fig. 61.

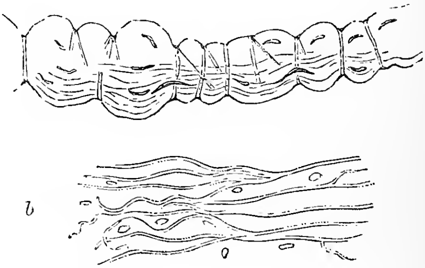

Fig. 61.—Magnified view of areolar tissue (from different parts) treated with acetic acid (Sharpey).

The white filaments are no longer seen, and the yellow or elastic fibres with the cell-nuclei come into view. *a*, a bundle of white fibres, which is swollen out by the effect of the acid, and presents a number of constricting bands. *b* shows the branching of the nearly straight elastic fibres of areolar tissue, and their union into a network.

rendered conspicuous under the microscope by means of acetic acid, which causes the white filaments to swell up and become indistinct, whilst the elastic fibres not being affected by that re-agent, come then more clearly into view (fig. 61, *b*). Moreover, they resist the action of boiling alkaline solutions of potash and soda, of moderate strength, which very speedily destroy the rest of the tissue.

A watery solution of magenta stains elastic fibres very intensely. The substance of which the elastic fibres is principally composed does not yield gelatine on boiling. It has been named *elastin*, and is one of the most resistant materials met with in the body. But it seems to be combined with some less resistant substance; for Pfeuffer found that after long digestion of elastic fibres in peptic or tryptic fluids, a portion of the fibre became swollen and partly dissolved, whilst the elastin remained for the most part in the form of separated particles.

Many observers have described transverse striation in elastic fibres (see fig. 59), especially in those that have been long macerated. It is not improbable that appearances of transverse striation, and also the tendency which the elastic fibres show to break across (seldom or never splitting longitudinally), are indications of the original formation of the fibres as rows of isolated particles, which subsequently become fused together.

Schwalbe ascribes sheaths to the elastic fibres. Some have thought them to be tubular; but, although probably less dense at the centre than at the periphery, the fibre seems to be solid throughout.

Arrangement of the Fibres in the areolar, fibrous, and elastic tissues respectively.—In the **areolar tissue** the bundles of white fibres intercross in all directions (fig. 62), and exhibit every degree of curvature. The bundles are exceedingly variable in size, the number of filaments in a bundle presenting a corresponding variation; and the laxity or density of the tissue depends chiefly upon the size of the bundles and the closeness with which they are packed.

The elastic fibres of areolar tissue run in the ground-substance between the white bundles, but when the latter are large and occupy almost the whole of the tissue the elastic fibres often appear to lie upon the surfaces of the bundles, and we even see here and there what appears to be an

elastic fibre winding round one of these bundles, and encircling it with several spiral turns. When acetic acid is applied, the fasciculus swells out between the constricting turns of the winding fibre, and presents a highly characteristic appearance (fig. 61, *a*). This remarkable disposition of the elastic fibres, which was pointed out by Henle, is not uncommon in certain parts of the areolar tissue ; it may be always

Fig. 62.

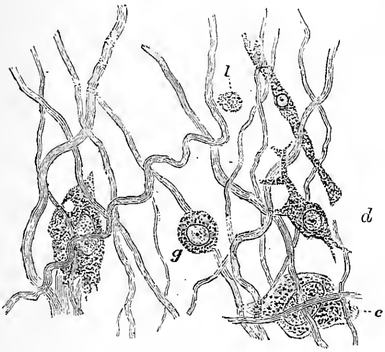

Fig. 62.—Subcutaneous connective tissue of a young guinea-pig; magnified 350 diameters.

d, branched corpuscle ; *e*, flattened corpuscle ; *g*, granular corpuscle ; *l*, leucocyte or migratory cell. The elastic fibres are not represented.

seen in that which accompanies the arteries at the base of the brain. It must be observed, however, that the encircling fibre sometimes forms not a continuous spiral, but several separate rings. In such a case the appearance may be explained on the supposition that the bundles in question are naturally invested with a delicate sheath (of ground-substance), which, like the elastic tissue, resists acetic acid, but, on the swelling up of the bundle under the operation of that agent, is rent into shreds or segments, mostly annular or spiral, which cause the constrictions. In other cases the union of branches of the cells around a bundle may be the cause of the appearance.

The areolæ, or interstices of the areolar tissue, are intercommunicating cleft-like spaces between the bundles and laminæ. They are not present in the immature tissue, in which the ground-substance is continuous throughout, but as the matrix becomes fibrillar the areolæ are formed, probably by the liquefaction of ground-substance.

In the **fibrous tissue** the bundles of white filaments run parallel, cohering very intimately. They either run all in one direction as in long tendons, or intersect each other in different planes as in some aponeuroses, or they take various directions and decussate irregularly with each other as in the dura mater. And when they run parallel to each other, as in tendon, they do not keep separate throughout their length, but send off slips to join neighbouring bundles and receive the like in turn ; so that successive cross sections of a tendon or ligament present different figures of the sectional areas of the bundles. A sheath of dense areolar tissue covers the tendons and ligaments on the outside (fig. 63, *a*), and a variable amount of the same tissue (*d*, *e*) lies between the fasciculi into which the smaller bundles are grouped, separating them from one another, and also occurring, in greater amount, between the largest fasciculi (*c*). It is in these areolar tissue septa that the blood-vessels and lymphatics of a tendon or ligament run.

The surface of a tendon or of any other part consisting of this texture, appears marked across the direction of the fasciculi with alternate light and dark streaks, which give it a peculiar aspect, not

unlike that of a watered ribbon. This appearance is owing to the wavy course of the filaments, for when the light falls on them their bendings naturally give rise to alternate lights and shadows.

The fibrous and areolar tissues thus agreeing in their ultimate structure, it is not to be wondered at that sometimes the limits between the two should be ill-defined, and that the one should pass by inconspicuous

Fig. 63.

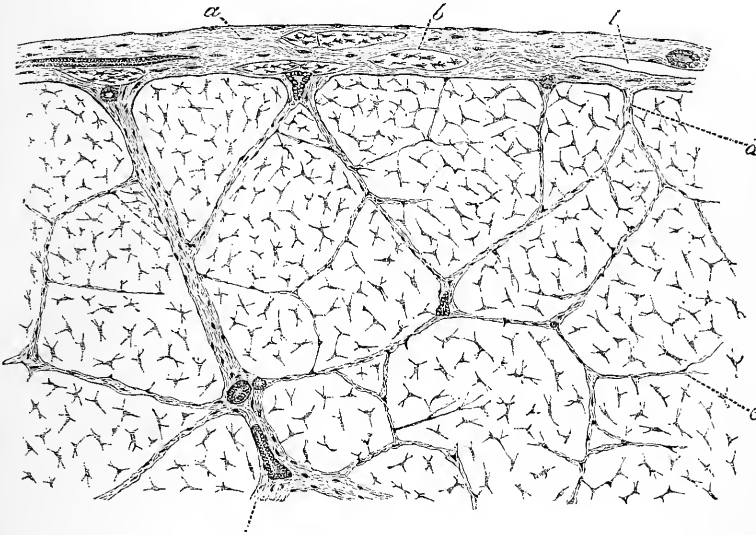

Fig. 63.—PART OF A MODERATELY LARGE TENDON IN TRANSVERSE SECTION (E. A. S.)

a, areolar sheath of the tendon, with the fibres for the most part running transversely, but with two or three longitudinal bundles, *b*; *l*, lymphatic cleft in the sheath; immediately over it a blood-vessel is seen cut across and on the other side of the figure a small artery is shown cut longitudinally; *c*, large septum of areolar tissue; *d*, smaller septum; *e*, still smaller septum. The irregularly stellate bodies are the tendon cells in section.

gradations into the other. Instances of such a transition may be seen in many of the fasciæ: these at certain parts consist of dense areolar tissue, but on being traced farther are seen gradually to become fibrous; and fasciæ, which in one body are areolar in character, may be decidedly fibrous in another.

In the **elastic tissue**, there is a great proportionate development of the elastic fibres, the white bundles being relatively few and indistinct, but considerable variation is met with in the proportion of the two kinds of elements. The white bundles are, for the most part, disposed irregularly and course in different directions, as in areolar tissue; but, in some elastic ligaments, there are bundles of white fibres, which run as in an ordinary ligament parallel with one another, and from end to end of the structure. The elastic fibres in an elastic ligament, are collected into smaller and larger groups or bundles (fig. 60), which are separated from one another by septa of the white tissue, but the latter also penetrates between the individual elastic fibres of the group.

The Cells or Corpuscles of Connective Tissue.—The cellular elements of connective tissue, are mostly lamellar in shape (fig. 62, *e*, and fig. 64), and lie imbedded in the ground-substance, being often applied to the surfaces of the bundles of white fibres. Where three or more bundles come into apposition, the connective tissue cells may

Fig. 64.

Fig. 64.—Two connective tissue corpuscles from the subcutaneous connective tissue; highly magnified. (E. A. S.)

The dark streak below *l*, in the right hand corpuscle, is a lamella which happens to be projecting towards the observer and is seen in optical section.

extend between the several bundles, and they then consist of not one lamella, but of two, three, or more which fit in between the bundles, the body of the cell occupying the larger interstice. The cells in some parts,

Fig. 65.

Fig. 66.

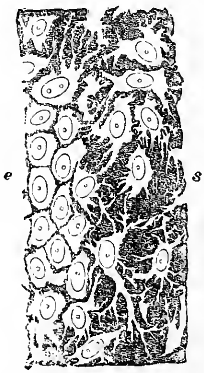

Fig. 65.—Ramified connective tissue corpuscles (E. A. S.); magnified 250 diameters.

(From a preparation stained with chloride of gold.)

Fig. 66.—Epithelioid and ramified cell-spaces of connective tissue (E. A S.). 340 diameters.

(From a preparation stained with nitrate of silver.)

The nuclei of the cells are faintly indicated.

united by their edges into patches, after the manner of an epithelium; but in other cases, the union takes place by means of branching pro-

cesses, so that the cells form a kind of network throughout the ground-substance, and a corresponding network is of course formed by the spaces in which the cells lie. These flattened connective tissue corpuscles are generally composed of comparatively clear cell-substance, with but a few granules scattered through it; they have a large oval nucleus with an intra-nuclear network and nucleoli.

According to Klein, "it can be shown that each connective tissue corpuscle is composed of two distinct substances: (*a*) a hyaline plate—*ground-plate*—which contains the oval nucleus, the substance of which is a dense network—intranuclear network; and (*b*) a second substance—a network of minute fibrils, *intracellular network*—arranged always more copiously at one side of the nucleus than at the other."

Besides these clear flattened cells, others are met with in the connective tissue, which are spheroidal and more decidedly granular, with rounder nuclei (fig. 62, *g*). Here again we must distinguish between those cells which have actual coarse granules in their protoplasm, and those the protoplasm of which is finely reticular, and merely appears granular under

Fig. 67.

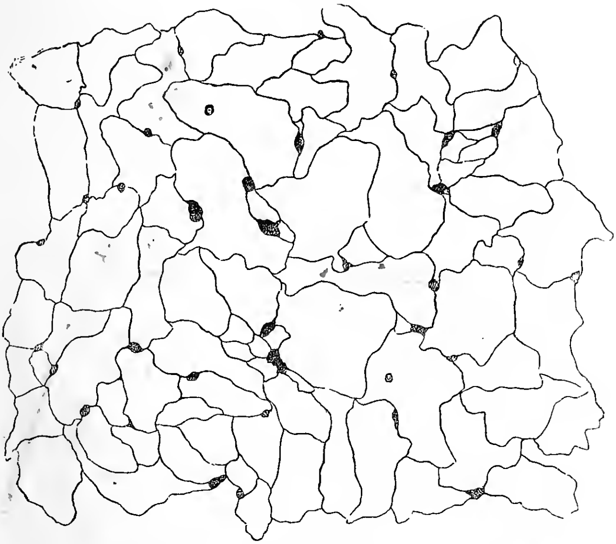

Fig. 67.—Epithelioid cells of connective tissue. From the surface of an aponeurosis treated with nitrate of silver. Highly magnified. (E. A. S.)

ordinary powers of the microscope. Although often classed together under the name of plasma-cells (Waldeyer), they are perfectly distinct elements, and it will be better therefore to reserve the name "plasma-cells" for the latter kind, especially since the reticulation of the protoplasm seems to be due to the accumulation of vacuoles containing fluid (lymph) within it, and to employ the name of granular cells for those which contain obvious granules. These are especially abundant near the blood-vessels, from which it might be inferred that they are derived from white blood-corpuscles which have migrated from the blood-vessels. Both

granular and plasma cells, are however, considerably larger than the ordinary migratory cells (fig. 62, *l*), which are also frequently met with in the connective tissue, and are known by their amœboid movement, which the connective tissue corpuscles proper do not exhibit in any appreciable degree. The plasma-cells are often irregular in shape, and may possess branching processes (fig. 62, *d*). Sometimes they are elongated into a fusiform shape, but cells of this form are not so common as was at one time supposed ; the appearance being frequently produced by flattened cells seen edge-ways.

In many membranous forms of connective tissue, the flattened cells form an epithelial-like covering to the surfaces of the membrane or membranes (fig. 67), and may even complete the latter by bridging over any gaps existing between the bundles of fibres forming the membrane. Such epithelioid tracts may be of considerable extent. It is often observable, that the cells at the margin of the patch have processes at their free border, which are connected with the ordinary scattered cells of the tissue (see fig. 66).

In **areolar tissue**, the connective tissue cells have no very definite arrangement. Both the cells and the spaces in which they lie may intercommunicate by their branches, and in this way it often happens where the tissue is thicker. that the system of cells and cell-processes, and of corresponding canals, may effect a communication between the superficial and deeper parts of the tissue. The cells of areolar tissue, are connected moreover with the flattened cells which line the smaller blood-vessels and lymphatics, and by means of this connection, and the continuity of the cell-spaces of the tissue, channels are provided for the flow of blood-plasma from the blood-vessels or towards the lymphatics. In addition to this, no doubt some of the plasma or lymph may soak through the ground-substance, or find its way through the lacunar interstices (areolæ) of the tissue.

Fig. 68.

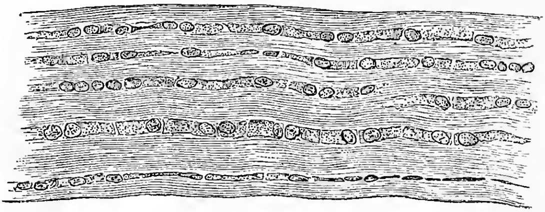

Fig. 68.—Tendon of mouse's tail, stained with logwood; showing chains of cells between the tendon-bundles. 175 diameters. (E. A. S.)

In **fibrous tissue,** (tendon and ligament), the cells, which are often called " tendon-cells," follow the parallel arrangement of the fibre-bundles, and are disposed in rows or chains (fig. 68), which may be easily seen if a very fine tendon, such as those in the tail of the mouse or rat, or a portion only of a larger one is examined under the microscope, and a little dilute acetic acid is cautiously added. A peculiar shape is impressed upon these cells by the close packing of the tendon bundles, for although they may look quadrangular or oblong when the tendon is viewed longitudinally (figs. 68, 69), yet when it is cut across, they have a stellate appearance (figs. 63, 70), for like other flattened connective tissue cells,

they send lamellar extensions into the interstices between the contiguous bundles, whilst the middle of each cell, containing the nucleus, lies in the

Fig. 69.

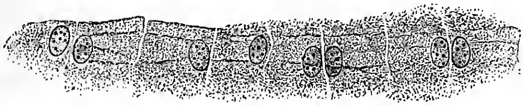

Fig. 69.—Eight cells from the same tendon as represented in Fig. 68. Magnified 425 diameters. (E. A. S.)

The nuclei, with their numerous nucleoli, were deeply coloured by the logwood. The dark lines on the surface of the cells are the optical sections of lamellar extensions directed towards or away from the observer.

angular space between three or more bundles. When the tendon-cells are viewed longitudinally, any of the lamellar extensions, which are directed either towards or away from the observer, appear as lines on the surface of the cell (fig. 69). The same appearance is often seen upon the flattened cells of the denser forms of areolar tissue, where the cells have been squeezed in between three or more bundles.

Each tendon-cell consists of a delicate protoplasmic body, thicker at the centre and thinning off in the extensions, and containing a flattened, round or oval, clear nucleus, with several nucleoli. The ends of adjacent

Fig. 70.

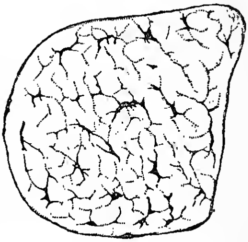

Fig. 70.—Transverse section of tendon of mouse's tail stained with logwood. 175 diameters. (E. A. S.)

The flattened processes of the tendon-cells (which are stained deeply by logwood) appear in section as lines, frequently coming off at right angles from the body of the cell. The bundles of fibres are not represented; they are very irregular, and but incompletely separated by the cell-processes.

cells are in close apposition, and form, as before noticed, long chains of cells in the tendon, and the nucleus is generally so situated towards one end of the cell as to be in close proximity to the nucleus of an adjacent cell; they thus present the appearance of being arranged in pairs (fig. 69). Here and there a third nucleus, with a small amount of protoplasm, may be seen interpolated between two such cells.

The lamellar extensions of the cells do not always end with an even line, but are themselves often prolonged into fine branches, which penetrate still further into the ground-substance which separates the fibre-bundles of the tendon from one another.

In the **pure elastic tissue,** such as that which constitutes the ligamentum nuchæ in animals and the ligamenta subflava in man, it is generally stated that cells are altogether absent. Schwalbe finds on the contrary numerous flat connective tissue cells scattered in the ground-substance which lies between the elastic fibres; the cells being often in close apposition with the elastic fibres, but never in continuity with them, as was described by Thin.

Vessels and Nerves of Connective Tissue.—Although blood-vessels, lymphatics, and nerves are everywhere conveyed in the **areolar tissue** to the places where they are to be distributed, very few blood-capillaries are destined for the tissue itself, although abundant lymphatic networks are present in many parts; especially in the subcutaneous, subserous and submucous tissues. It is uncertain whether nerves terminate in the areolar tissue. It may be cut in a living animal apparently without giving pain, except when the instrument meets with those branches of nerves which traverse the tissue on their way to other parts.

The **fibrous tissue** receives blood-vessels, but in general they are inconsiderable both in number and size compared with the mass of tissue to which they belong. In tendons and ligaments with longitudinal fasciculi, the chief branches of the vessels run parallel with and between the larger fasciculi, and, sending communicating branches across them, eventually form a very open network with large oblong meshes. Some fibrous membranes, as the periosteum and dura mater, are much more vascular; but the vessels seen in these membranes do not strictly belong to them, being destined for the bones which they cover.

Lymphatics are contained in great abundance, as Ludwig and Schweigger-Seidel showed, in the enveloping areolar-tissue sheaths of tendons and aponeuroses, where they form plexuses with polygonal meshes. In addition to these, a close network of lymphatic vessels with elongated meshes may be injected in the deeper parts of the tendons, where they run in the penetrating areolar tissue. Sometimes, as in the central tendon of the diaphragm, lymphatic spaces separate the tendon bundles from one another. A connection no doubt subsists between these lymphatics and the cell-spaces of the fibrous tissue: and it has been suggested that the lymphatic vessels of the tendons are partly concerned in the removal of lymph from the muscles, in which the existence of lymphatic vessels has not hitherto been recognized.

The penetrating areolar tissue of tendons, like the same tissue elsewhere, possesses areolæ, which here take the form of elongated clefts, and these may also partly serve for the passage of lymph.

Many tendons and ligaments, and some fibrous membranes, have been shown to possess nerve-fibres, which course for the most part in a direction parallel with the fasciculi and may terminate in a special manner within these tissues, as will be noticed when the peripheral distribution of nerves is described.

As to **elastic tissue,** the yellow ligaments, which contain this in its purest form, are but scantily supplied with blood-vessels, those that are present running in the interstitial areolar tissue between the elastic bundles. The lymphatic vessels also course for the most part longitudinally in the interstitial areolar tissue, being connected here and there by transverse branches, and in addition to these vessels the lymph may be conveyed by means of the elongated areolæ of the same tissue. Neither blood-vessels nor lymphatic vessels actually penetrate into the small bundles of elastic fibres, although the lymphatic vessels often lie close against the surface of the bundles.

SPECIAL VARIETIES OF CONNECTIVE TISSUE.

1.—At an early period of development connective tissue consists of a pellucid jelly and nucleated corpuscles. The soft watery jelly contains the chemical principle of mucus, or *mucin*, and, in much less proportion, *albumin*, but not gelatin. In the general course of development of the tissue, fibres, both white and elastic, are formed in the soft matrix, and finally obscure or obliterate this substance in a great measure. But in certain cases the course is different. The cells may disappear, only the jelly remaining, as in the vitreous humour of the eye; or the corpuscles

Fig. 71.

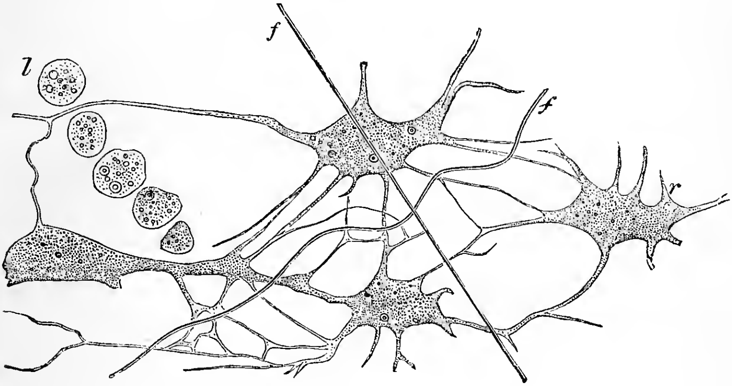

Fig. 71.—Jelly of Wharton (Ranvier)

r, ramified cells intercommunicating by their branches; *l*, a row of leucocytes or migratory cells; *f*, *f*, fibres coursing through the ground-substance.

may branch out and join together in form of a network in the jelly, with the nuclei persisting at the spots whence the threads diverge. The areolar tissue surrounding and imbedding the vessels in the umbilical cord of the fœtus consists of fusiform and ramified corpuscles associated with white fibrillar bundles and elastic fibres, along with a quantity of the original soft matrix, which is persistent at the time of birth. The tissue is here known as the jelly of Wharton (fig. 71).

Connective tissue of this nature is known as **jellylike** or **mucous tissue**.

2.—In other cases the matrix disappears or liquefies: and the ramified corpuscles unite together into a reticular or fine trabecular structure (fig. 72): either retaining their nuclei as at *a*, or losing them and then forming a fine network of simple fibres without nuclei as at *b*. Sometimes the processes of the cells are flattened out, and then sections of the tissue have a somewhat honeycombed appearance.

That the tissue is constructed of ramified corpuscles is shown by its withstanding boiling in water, whilst it readily dissolves in hot alkaline solutions, whereas if the fibres composing the network were of the white or of the elastic variety, they would behave differently under such treatment. Nevertheless as Bizzozero has pointed out, the branched

cells of this tissue are, in some situations at least, if not in all, wrapped round small anastomosing bundles of connective tissue fibres.

To a tissue which is thus formed of branched cells united into a network, the term **retiform or reticular tissue** is applied: it is also known as **adenoid tissue.**

Fig. 72.

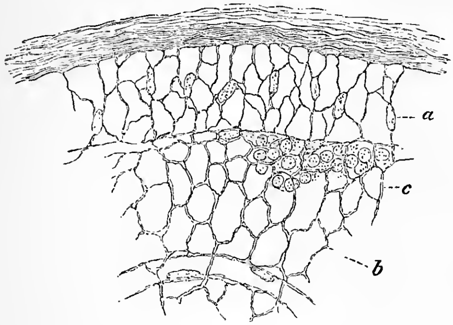

Fig. 72.—THIN SECTION FROM THE CORTICAL PART OF A LYMPHATIC GLAND, MAGNIFIED. (His.)

a, *b*, network of fine trabeculæ formed by retiform or adenoid tissue, from the meshes of which the lymph-corpuscles have been washed out, except at *c*, where they are left.

In many situations the meshes of the retiform tissue are occupied by numerous corpuscles which closely resemble the pale blood- or lymph-corpuscles, but have a relatively larger nucleus, and less protoplasm than those. They are known as *lymphoid cells*, and the tissue containing them is termed **lymphoid or lymphatic tissue.** In this form, retiform tissue is found composing the greater part of the lymphatic glands, and other structures allied to them, such as the solitary and agminated glands of the intestine, and the similar structures in the tonsils and elsewhere. Moreover, the alimentary mucous membrane is in great measure composed of the same tissue, and it occurs also in other mucous membranes and, in the form either of elongated tracts or of isolated nodules, in many parts of the serous membranes. In the spleen, the interstices of the retiform tissue are for the most part occupied by blood, instead of by lymph as elsewhere. In organs into the construction of which this tissue enters, it serves as a supporting framework to those parts of the organ into which connective tissue of the ordinary kind does not penetrate.

3.—Another special variety of connective tissue is met with in the form of delicate membranes, and was formerly supposed to be quite homogeneous in structure. These membranes have, however, in many cases been shown to be made up of flattened cells, in close apposition, which can be brought to view by staining with nitrate of silver. This is the case with the so-called **basement membranes** or **membranæ propriæ**, which are found under the epithelium of many mucous membranes, and outside the epithelium of secreting glands. They form therefore examples of an epithelioid arrangement of connective tissue cells. In other cases the membranes in question are of an elastic nature, *e. g.* the posterior elastic lamina of the cornea.

DEVELOPMENT OF CONNECTIVE TISSUE.

Those parts of the early embryo in which connective tissue is subsequently to be developed, are at first composed entirely of embryonic cells, to all appearance similar to those which constitute the mesodermic layer generally. The first change of importance that occurs is the development of blood-vessels

from some of these cells in the manner that has already been partly explained (p. 34), and will be further treated of when those vessels have come under consideration. Soon after the development of these primitive blood-vessels the embryonic cells become more separated, but retain for the most part a connection with one another by interjoining processes; and the interstices between the cells are now found to be filled with a clear fluid, which is either produced by the cells themselves, or derived directly by transudation from the blood-vessels. This muco-albuminous fluid subsequently acquires a firmer consistence, and eventually remains as the ground-substance.

In this ground-substance fibres become developed of the two kinds, white and elastic, but the manner in which they are formed is by no means clear; and two distinct and opposed views are held by histologists upon the subject. According to the one view, the bundles of white fibrils are produced by a direct conversion of the protoplasm of some of the cells, the others remaining as the permanent connective tissue corpuscles; or it may be that some of the latter represent embryonic cells, layers of whose protoplasm have been successively converted into fibrillar tissue, the cells, meanwhile, after each such conversion, growing again to their original size, and at length remaining in contact with the bundle of fibres which they have assisted to form. Similarly the elastic fibres are believed to be formed of the processes of some others of the embryonic cells, which become connected with processes from other cells, and undergoing a chemical transformation, produce the networks of elastic fibres. According to the other view the fibres, both white and elastic, are formed by a deposit in the intercellular substance, and not by a direct change of the protoplasm of the cells, with which indeed they are not connected; although it is not impossible that the deposition may in some way or other be influenced, or even caused by the pre-existing cells.

In favour of this latter view may be instanced the jelly of Wharton, which is merely connective tissue in a particular phase of development, and in which the fibres of both kinds can be seen coursing through the jelly-like intercellular substance, apart entirely from the cells (see fig. 71, *f*). And further it may be mentioned that, when white fibres of connective tissue are developed in cartilage, it is in the intercellular substance that they appear, and, so far as can be seen, they are quite unconnected with cells. In the case of the elastic fibres, these, as shown by Ranvier, first appear in the form of rows of granules or globules, which subsequently become fused together end to end, and are not at any time connected with cells (Fig. 73). To form an elastic membrane, in place of being arranged in lines the globules are deposited in small patches, and by

Fig. 73.

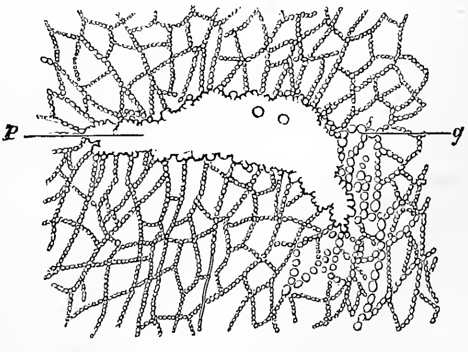

Fig. 73. — Development of elastic tissue by deposition of fine granules (Ranvier).

g, moniliform fibres formed of rows of "elastin" granules; *p*, flat platelike expansion of elastic substance formed by the fusion of "elastin" granules.

their fusion the membrane is formed (*p*). In elastic cartilage the granules first make their appearance, it is true, in the immediate neighbourhood of the cartilage-cells; but although this renders it probable that the deposition of the granules is influenced by the cells, it does not prove that they are formed by a direct conversion of the cell-protoplasm. Indeed, the subsequent extension of the fibres into those parts of the matrix which were previously clear of them, and in which no such direct conversion of

cell-protoplasm seems possible, is a strong argument in favour of the deposition hypothesis.

The view which supposes that a direct conversion of the protoplasm of the connective tissue cells takes place into fibres, both white and elastic, has of late years been widely adopted, but it seems to rest less upon observation than upon a desire to interpret the facts in accordance with the conceptions of Beale and M. Schultze, according to which every part of an organised body consists either of protoplasm (formative matter), or of material which has been protoplasm (formed material), and the idea of a deposition or change occurring outside the cells in the intercellular substance is excluded. But it is not difficult to show that a formation of fibres may occur in soft substances in the animal organism, independently of the direct agency of cells, although the materials for such formation may be furnished by cells. Thus in those cœlenterate animals in which a low form of connective tissue first makes its appearance, this is distinguished by a total absence of cellular elements, the ground-substance being first developed and fibres becoming formed in it. Again, the fibres of the shell-membrane of the bird's egg are certainly not formed by the direct conversion of the protoplasm of the cells which line the oviduct, although it is probably in matter secreted by those cells, and through their agency, that the deposit occurs in a fibrous form.

The formation of the special varieties of connective tissue has already been considered (see p. 69).

Regeneration.—Connective tissue appears to be readily regenerated, although the new cicatricial tissue which is formed in place of that which has been removed by the knife or by disease, is not always of the same character, either as regards its cells or fibres, as the tissue it replaces. In the course of time the new tissue may assimilate itself somewhat to the old, but seldom to such an extent that the scar cannot be detected.

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ADIPOSE TISSUE.

The human body in the healthy state contains a considerable amount of fatty matter of different kinds. It exists in several of the secretions—in some constituting the chief ingredient; and it enters into the composition of many of the textures. But by far the greater part of the fat of the body is inclosed in small cells or vesicles, which, together with their contained matter, constitute the adipose tissue.

Distribution.—This tissue is not confined to any one region or organ, but exists very generally throughout the body, accompanying the still more widely distributed areolar tissue in most, though not in all parts in which the latter is found. Still its distribution is not uniform, and there are certain situations in which it is collected more abundantly. It forms a considerable layer underneath the skin, and, together with the subcutaneous areolar tissue in which it is lodged, constitutes in this situation what has been called the *panniculus adiposus.* It is collected in large quantity round certain internal parts, especially the kidneys. It is seen filling up the furrows on the surface of the heart, and imbedding the vessels of that organ beneath its serous covering; and in various other situations it is deposited beneath the serous membranes, or is collected between their folds, as in the mesentery and omentum, at first generally gathering along the course of the blood-vessels and at length accumulating very copiously. Collections of fat are also common round the joints, lying on the outer surface of the synovial membrane, and filling up inequalities; in many cases lodged in folds of the

Fig. 74.

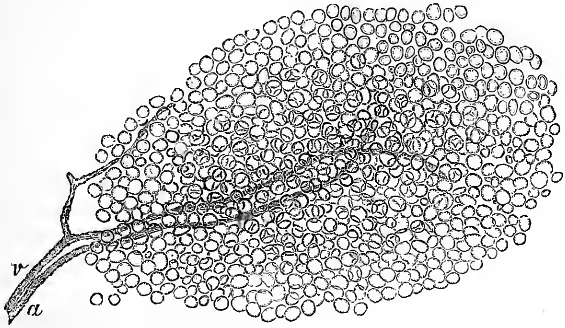

Fig. 74. A small fat-lobule from the subcutaneous tissue of the guinea-pig, magnified about 20 diameters. (E. A. S.)

a, small artery distributed to the lobule; *v,* small vein; the capillaries within the lobule are not visible.

membrane, which project into the articular cavity. Lastly, the fat exists in large quantity in the marrow of bones. On the other hand, there are some parts in which fat is never found in the healthy condition of the body. Thus it does not exist in the subcutaneous areolar tissue of the eyelids and penis, nor in the lungs except near their roots, nor within the cavity of the cranium.

Structure.—When subjected to the microscope, the adipose tissue is seen to consist of small vesicles, filled with an oily matter, and for the most part lodged in the meshes of the areolar tissue. The vesicles are most commonly collected into little lobular clusters (fig. 74), and

these again into the little lumps of fat which we see with the naked eye, and which in some parts are aggregated into round or irregular masses of considerable magnitude. Sometimes the vesicles, though grouped together, have less of a clustered arrangement; as when they collect alongside of the minute blood-vessels of thin membranous parts.

In well-nourished bodies the vesicles or fat-cells are round or oval (fig. 75), unless where packed closely together, in which case they acquire an angular figure, and bear a striking resemblance to the cells of vegetable tissues. The greater number of them are from $\frac{1}{300}$th to $\frac{1}{600}$th of an inch in diameter, but many exceed or fall short of this measurement. Each one consists of a very delicate envelope (*m*), inclosing the oily matter, which, completely filling the envelope, appears as a single drop (*f, g*). It often happens that a part of the fatty contents solidifies in the cell after death, forming a bunch of delicate needle-shaped crystals (fig. 75, *c r*).

The envelope is the remains of the original protoplasm of the cell: it

Fig. 75.

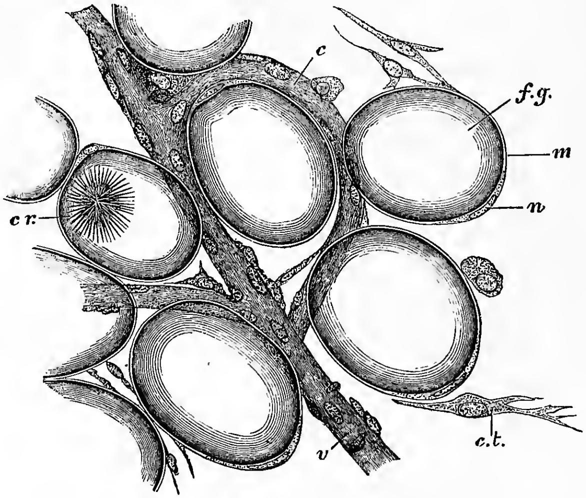

Fig. 75. A FEW CELLS FROM THE MARGIN OF THE FAT-LOBULE REPRESENTED IN THE PRECEDING FIGURE: HIGHLY MAGNIFIED. (E. A. S.)

f g, fat globule distending a fat-cell; *n*, nucleus; *m*, membranous envelope of the fat-cell; *c r*, bunch of crystals within a fat-cell; *c*, capillary vessel; *v*, venule; *c t*, connective tissue cell; the fibres of the connective tissue are not represented.

is generally quite transparent, and apparently homogeneous. According to some authorities it consists of two parts, a delicate structureless external membrane, and a layer of finely granular protoplasm immediately surrounding the fat. The nucleus (*n*) is always present in the protoplasm, but is often so flattened out by the pressure of the inclosed oil-drop as to be visible only with difficulty.

The areolar tissue connects and surrounds the larger lumps of fat, but forms no special envelope to the smaller clusters; and although fine fasciculi and filaments of that tissue pass irregularly over and through the clusters, yet it is probable that the vesicles are held together in these

groups mainly by the fine network of capillary vessels distributed to them. In the marrow the connective tissue fibrils are but few in number or may, it is said, be absent altogether.

The adipose tissue is copiously supplied with **blood-vessels.** The larger branches of these pass into the fat-lumps, where they run between the lobules and subdivide, till at length a little artery and vein are sent to each small lobule (fig. 74, *a*, *v*), dividing into a network of capillary vessels, which pass between the vesicles in all directions, supporting and connecting them. The **lymphatics** of the fat are in close relation to the blood-vessels, accompanying and occasionally completely enclosing them as they enter the lobule. No nerves have been seen to terminate in this tissue, although nerves destined for other textures may pass through it. Accordingly it has been observed that, unless when such traversing nervous twigs happen to be encountered, a puncturing instrument may be carried through the adipose tissue without occasioning pain.

Development.—The fat first appears in the human embryo about the fourteenth week of intra-uterine life. It is deposited in the form of minute granules or droplets in certain cells of the connective tissue (figs. 76, 77, *f*, *f′*): these droplets increase in size, and eventually run together, so as to form one large drop in each cell. By further deposition the cell becomes swollen out to a size far beyond that which it possessed originally, and its protoplasm remains as a delicate envelope surrounding the fat-drop. By the end of the fifth month the fat-cells have largely increased in number, and have become collected into small groups.

Fig. 76.

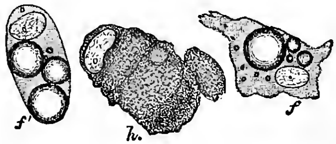

Fig. 76.—Deposition of fat in connective tissue cells of the new-born rat. (E. A. S.)

f, *f′*, fat cells; *h*, hæmapoietic cell.

The deposit of fat within the cells is preceded and accompanied by the formation of a rich network of capillary blood-vessels (fig. 77), which are produced by a transformation of other cells of the tissue in the manner previously described (p. 34).

Fig. 77.

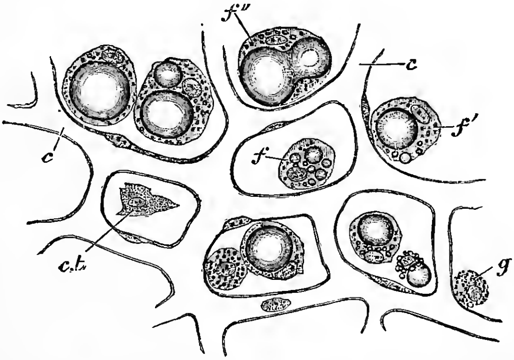

Fig. 77. Deposition of fat in connective tissue cells. (E. A. S.)

f, a cell with a few isolated fat-droplets in its protoplasm; *f′*, a cell with a single large and several minute drops; *f″*, fusion of two large drops; *g*, granular cell, not yet exhibiting any fat deposition; *c t*, flat connective tissue corpuscle; *c*, *c*, network of capillaries.

The fat is often deposited in the granular cells of the connective tissue, these being usually found in great abundance in those situations in which fat is becoming developed (fig. 77). Sometimes, however, the deposition takes place in the more ordinary connective tissue cells (fig. 76, *f*), or in cells which are apparently intermediate between these and the granular cells, being rounded like the latter, but consisting of a much clearer protoplasm (fig. 76, *f′*). When deposited in ramified or flattened cells these acquire a spherical shape as they enlarge, in consequence of the distension produced by the accumulating fat.

The fat in some parts, and especially in the serous membranes, is formed at the expense of pre-existing lymphatic tissue, the lymphoid cells probably becoming enlarged and transformed into fat cells, whilst a considerable development of blood-vessels accompanies the change. A similar transformation is also witnessed in the thymus gland, which, in the fœtus and infant, is chiefly composed of lymphoid tissue, but as growth proceeds becomes wholly converted into a mass of fat.

The superficial resemblance which adipose tissue often bears to many glands, in its lobulated structure and the arrangement of its blood-vessels, has led some histologists to look upon the fat-cell as a corpuscle of specific nature, and totally distinct from any other kind of cell met with in the connective tissue. But against this view it may be urged that the situations in which fat is deposited are, previously to its appearance, in no way distinguishable from the rest of the areolar tissue; that the cells in which it is produced are, so far as can be seen, the same as those which are met with in almost all parts of the areolar tissue; and further, that when from any natural cause the fat is entirely removed from the cells of a part and not again deposited in them, the part eventually acquires all the ordinary characteristics of the areolar tissue. The great development of blood-vessels in adipose tissue is obviously related to the function which it subserves in storing up the fatty materials derived from the food in such a form and situation as to be readily re-absorbed into the circulation when needed. Moreover, fat may be deposited in other kinds of connective tissue than the areolar, and even in the cells of some epithelia.

PIGMENT.

An accumulation of coloured pigment-granules is met with in many cells of the animal body, but most frequently in epithelium-cells and in cells belonging to the connective tissue. A well-marked example of pigmented epithelium-cells in the human body is afforded by the black coating which forms the external layer of the retina of the eye, and covers the posterior surface of the iris. Dark pigment is also met with in

Fig. 78.

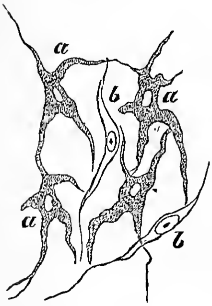

Fig. 78.—Ramified cells, from the tissue of the choroid coat of the eye; magnified 350 diameters (Kölliker).

a, cells with pigment; *b*, colourless fusiform cells.

the deeper layers of the cuticle, especially in the coloured races, and in certain epithelial cells of the membranous labyrinth of the ear, and the olfactory region of the nose (combined in the latter case with brownish yellow pigment).

In the connective tissue the pigment is met with in enlarged and irregularly branched corpuscles which are termed **pigment-cells.** Such ramified cells are very common in many animals. In the human body cells of this description are found in the dark tissue on the outer surface of the choroid coat, (fig. 78, *a a*), in the iris, where they are often variously coloured, and on the pia mater covering the upper part of the spinal cord. Pigment is also found in some of the

ramified cells which form part of the retiform tissue of the medullary substance of lymphatic glands, and occasionally in some of the similar cells of the spleen. It may also be seen in migratory cells, but this is more common in pathological conditions.

The pigment, strictly so called, which is contained within the cells, consists of black or brown granules or molecules of a round or oblong shape, and almost too small for exact measurement. These molecules are densely packed together in some cells; in others they are more scattered, and then it may be seen that there is a certain amount of colourless matter included along with them. When they escape from the ruptured cells, they exhibit very strikingly the "Brownian" molecular movement; and in consequence of this movement the apparent figure of the particles is subject to change. It is worthy of remark, that when viewed singly with a very high magnifying power they look transparent and almost colourless, and it is only when they are heaped together that their dark colour distinctly appears. The nucleus of the pigment-cell is not coloured, but is very often hidden from view by the black particles.

In the lower animals remarkable movements are often observed in the ramified pigment-cells, *e.g.*, those of the frog's skin. In these the dark particles of pigment are at one time dispersed through the whole cell and its branches, but at another time they gather into a heap in the central part, leaving the rest of the branched cell vacant, but without alteration of its figure. In the former case the skin is of a dusky hue; in the latter, pale. The aggregation of the pigment-molecules can be excited through the nerves, both directly and also in a reflex manner, as by the stimulus of light upon the retina.

CARTILAGE.

This is the well-known substance commonly called "gristle." The following are its more obvious characters. When in mass, it is opaque and of a pearly or bluish white colour, in some varieties yellow; but in thin slices it is translucent. Although it can be easily cut with a sharp knife, it is nevertheless of very firm consistence, but at the same time highly elastic, so that it readily yields to pressure or torsion, and immediately recovers its original shape when the constraining force is withdrawn. By reason of these mechanical properties, it serves important purposes in the construction of some parts of the body.

In the early embryo the skeleton is, in great part, cartilaginous; but the cartilage forming its different pieces, which have the outward form of the future bones, in due time undergoes ossification or gives place to bone, in the greater part of its extent at least, and hence this variety of cartilage is named "temporary."

Of the permanent cartilages a great many are in immediate connection with bone, and may be still said to form part of the skeleton. The chief of these are the articular and the costal cartilages; the former cover the ends or surfaces of bones in the joints, and afford these harder parts a thick springy coating, which breaks the force of concussion and gives ease to their motions; the costal or rib-cartilages form a considerable part of the solid framework of the thorax, and impart elasticity to its walls. Other permanent cartilages enter into the formation of the external ear, the nose, the eyelids, the Eustachian

tube, the larynx, and the windpipe. They strengthen the substance of these parts without undue rigidity; maintaining their shape, keeping open the passages through them where such exist, and giving attachment to moving muscles and connecting ligaments.

Cartilages, except those of the joints, are covered externally with a vascular fibrous membrane named the *perichondrium.*

When a very thin slice of cartilage is examined with the microscope, it is seen to consist of nucleated cells, disseminated in a solid mass or matrix (fig. 80). The matrix is sometimes transparent, and to all appearance homogeneous; sometimes dim and very faintly granular, like ground glass: both these conditions occur in *hyaline cartilage*, which may be regarded as the most typical form of the tissue. Two varieties exist in which the matrix is pervaded to a greater or less extent by fibres. In the one named *elastic* or *yellow fibro-cartilage*, the fibres are similar to those of elastic tissue; in the other, named *white fibro-cartilage*, they are of the white kind as in ordinary ligament.

HYALINE CARTILAGE.

Structure.—In hyaline cartilage the matrix, as just stated, is uniform, and, when examined fresh, usually appears free from fibres. Like the ground-substance or matrix of connective tissue, it becomes stained brown by nitrate of silver and subsequent exposure to the light. The cells consist of a rounded, oval, or bluntly angular *cell-body* of

Fig. 79.

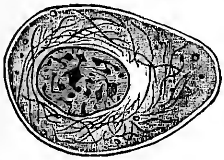

Fig. 79.—A CARTILAGE CELL IN THE LIVING STATE, FROM THE SALAMANDER. HIGHLY MAGNIFIED (Flemming).

translucent protoplasm, embedded in which are fine curvilinear interlacing filaments and minute granules (fig. 79), with a round *nucleus*, which is either clear with one or more *nucleoli*, or, more commonly, is occupied by a network of nucleoplasm, which produces under a low power of the microscope a granular effect. The cell-body lies in a cavity of the matrix, which, in its natural condition, it entirely fills. This cavity is bounded and inclosed by a transparent *capsule*, which is seldom obvious to the eye, for it coheres intimately with the surrounding matrix, with which it agrees in nature, and cannot usually be distinguished without the aid of re-agents.

By exposure to water and some other liquids, as well as to the action of electric shocks, the cell-body shrinks away from the inside of the capsule, and assumes a jagged or otherwise irregular figure, and then may hide the nucleus (fig. 82). It often contains larger or smaller fat-globules (fig. 80, *g*).

The cells of cartilage appear to contain glycogen, for they are coloured reddish brown by iodine (Neumann).

They are rarely dispersed singly in the matrix; most commonly occurring in groups of two or more. When disposed in pairs (as at *a*, fig. 80) the cells are generally triangular or pyramidal in form with rounded angles, and with their bases opposite one another; in the larger groups (*b*) the cells have a straight outline where they adjoin or approach one another, but at the circumference of the group their outline is rounded. Towards the surface of the cartilage the groups are

generally flattened conformably with the surface, appearing narrow and almost linear when seen edgeways, as in a perpendicular section (fig. 81, *a*).

Various observers, and especially Tillmanns, have shown that the matrix of hyaline cartilage can be broken up after long maceration, and with the aid of pressure, into fine fibrils. According to Cresswell Baber, these fibres are vertical to the surface in articular cartilage, and parallel with the long axis in rib cartilage. Their chemical nature is not, however, very clear, nor is it certain how far the appearances correspond with any structure naturally present; but if, as Kühne and Merochowetz assert, gelatin and mucin can be obtained from the matrix of cartilage, the fibres in question may be chemically of the same nature as the white fibres of connective tissue, the mucin belonging to the ground-substance in which they are embedded.

Fig. 80.

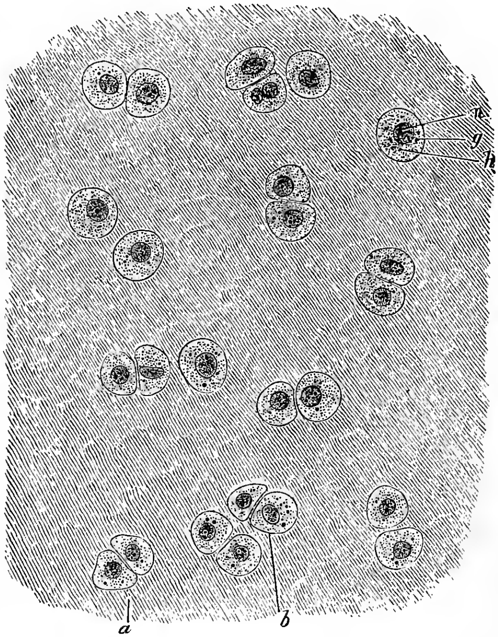

Fig. 80.—Articular cartilage from head of metatarsal bone of man (osmic acid preparation). The cell-bodies entirely fill the spaces in the matrix. 340 diameters. (E. A. S.)

a, group of two cells; *b*, group of four cells; *h*, protoplasm of cell, with *g*, fatty granules; *n*, nucleus.

Other histologists have described a network of exceedingly fine ramified canals penetrating the cartilage matrix, and effecting a communication between the cell spaces. Up to the present time, however, the existence of such anastomosing channels has not been conclusively proved, although often assumed in order to explain the manner in which nutritive plasma penetrates the matrix of cartilage to reach the cells. Budge endeavoured to demonstrate the existence of canaliculi by forcing coloured injecting fluid into the substance of cartilage, but the result of the experiment was not conclusive. It has also been attempted to show them by the so-called natural method of injection, that is by allowing indigo-carmine (which has an intensely blue colour) to mix with the circulating blood of animals, which after a time are killed and the cartilages examined. Proceeding in this way, Gerlach was unable to see any blue channels in the cartilage matrix, while Arnold, on the other hand, obtained results from which he was led to infer the existence of minute cleft-like spaces throughout the matrix connected by fine radiating canaliculi on the one hand with the lymphatics in the perichondrium, and on the other hand with the cell-spaces of the cartilage.

Such is the structure of hyaline cartilage in general, but it is more or less modified in different situations.

In *articular cartilage*, the matrix in a thin section appears dim, like ground glass, having sometimes an almost granular aspect. The cells and cell-groups are smaller and more dispersed, as a rule, than in rib-cartilage. As is the case also with the cartilage of the ribs, the groups are flattened at and near to the surface, and lie parallel with it (fig. 81, *a*);

Fig. 81.

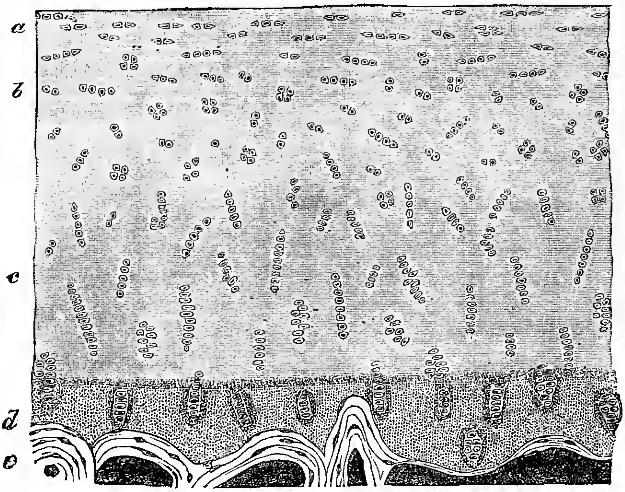

Fig. 81.—Vertical section of articular cartilage covering the lower end of the tibia (human). Magnified about 30 diameters. (E. A. S.)

a, cells and cell-groups flattened conformably with the surface; *b*, cell-groups irregularly arranged; *c*, cell-groups disposed perpendicularly to the surface; *d*, layer of calcified cartilage; *e*, bone.

deeper and nearer the bone, on the other hand, they are narrow and oblong, like short irregular strings of beads, and are mostly directed vertically (fig. 81, *c*). It is well known that articular cartilages readily break in a direction perpendicular to their surface, and the surface of the fracture appears to the naked eye to be striated in the same direction, as if they had a columnar structure; this may be due to the vertical arrangement of the rows of cells, or to the substance of the matrix being disposed in a fibrous or columnar manner (Leidy). It was formerly held that the free surface of articular cartilage is covered with epithelium, but no such covering really exists. It is easy, no doubt, to peel off a thin film from the surface of the cartilage of the head of the humerus or femur; but this superficial layer is really part of the cartilage, and its broad patches of cells with the intermediate matrix are not to be mistaken (fig. 82).

Near the margin of the articular cartilages connective tissue is prolonged a certain way into them from the synovial membrane, and the cartilage-cells acquire processes and present transitions to the connective-tissue corpuscles of that membrane (fig. 83).

The matrix of articular cartilage rarely, or perhaps never, becomes converted into fibro-cartilage, nor is it prone to ossify like rib-cartilage.

But a deposit of calcareous granules may occur in the deeper parts of the articular cartilage near the bone, the deposit first showing itself

Fig. 82.

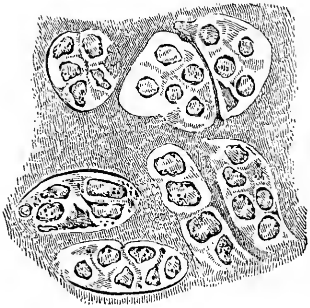

Fig. 82.—A THIN LAYER PEELED OFF FROM THE SURFACE OF THE CARTILAGE OF THE HEAD OF THE HUMERUS, SHOWING FLATTENED GROUPS OF CELLS (Sharpey).

The shrunken cell-bodies are distinctly seen, but the limits of the capsular cavities where they adjoin one another are but faintly indicated. Magnified 400 diameters.

around the groups of cartilage cells (fig. 81, *d*). This change may also happen at the symphyses. When the earthy matter is extracted by means of an acid, the tissue which remains has all the characters of cartilage.

In the *costal cartilages*, the cells, which are of considerable size, are also collected in groups, larger for the most part than those found in articular cartilage. Near the exterior of the cartilage they are flattened, and lie parallel with the surface. As to those situated more inwardly, we can sometimes observe, in a transverse slice, that they form oblong groups disposed in lines radiating to the circumference; but this arrangement is not constant, and they often appear quite irregular. The cells, with the exception of those lying upon the surface, frequently contain drops of oil, the nucleus being often altogether concealed by the fat. The matrix is clear, except where fibres have been developed in it, in which parts it is opaque and yellowish. Such fibrous patches

Fig. 83.

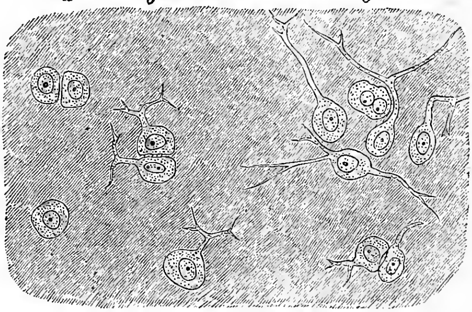

Fig. 83.—BORDER OF ARTICULAR CARTILAGE SHOWING TRANSITION OF CARTILAGE CELLS INTO CONNECTIVE-TISSUE CORPUSCLES. FROM HEAD OF METATARSAL BONE, HUMAN. ABOUT 340 DIAMETERS (E. A. S.).

a, ordinary cartilage cells; *b*, *b*, with branching processes.

are very frequent; the fibres are fine, straight, and parallel, appearing transparent when few together; they are not swollen by acetic acid. It is not uncommon to find the rib-cartilages extensively ossified.

The description given of the microscopic characters of the costal cartilages will apply with little variation to the ensiform cartilage of the sternum, to the cartilages of the larynx and windpipe, except the epiglottis and cornicula laryngis, and to the cartilages of the nose. With the exception of the last, these resemble the rib-cartilages also in their tendency to ossify.

The characters of the temporary cartilages, which are hyaline, will be noticed in the account of the formation of bone.

ELASTIC OR YELLOW CARTILAGE.

The epiglottis and cornicula of the larynx, the cartilages of the ear and of the Eustachian tube, differ so much from the foregoing, both in intimate structure and outward characters, that they have been included in a class apart, under the name of the "elastic," "yellow," or "spongy" cartilages. These are opaque and somewhat yellow, are more flexible and tough than the ordinary cartilages, and have little tendency to ossify. They are made up of cells and a matrix, but the latter is everywhere pervaded with fibres (fig. 84), except in a small area or narrow zone (shaded in the figure) left round each of the cells. The fibres resist the action of acetic acid; they are in many parts short, fine, and confusedly intersecting each other in all directions, like the filaments in a piece of felt; in such parts the matrix has a rough indistinctly granular look, but sometimes this appearance is due to the fact that the elastic fibres are incompletely developed, the granules which are to form them having not yet run together into fibres (fig. 85, *b*). Sometimes the fibres are longer (fig. 85, *c*) but they still intercommunicate at short distances.

Fig. 84.

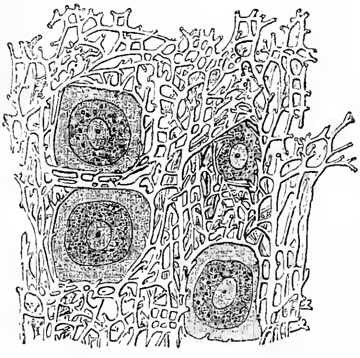

Fig. 85.

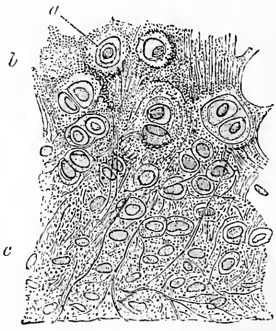

Fig. 84.—Section of the elastic cartilage of the ear. Highly magnified (Hertwig).

Fig. 85.—Section of part of the cartilage of the epiglottis (Ranvier).

a, cartilage cell in clear area; *b*, granular-looking matrix near the middle of the cartilage, the granular appearance being due partly to the fine reticulum of elastic fibres, partly to the presence of granules of elastic substance in the matrix; *c*, clearer matrix with longer fibres.

In large animals such as the ox, where the fibres of ordinary elastic tissue attain a considerable size, those of elastic cartilage are also very large with comparatively wide meshes, occupied of course by the hyaline ground-substance.

WHITE FIBRO-CARTILAGE.

This is a substance consisting of a mixture of the fibrous and cartilaginous tissues, and so far partaking of the qualities of both. Like hyaline cartilage, it possesses firmness and elasticity, but these properties are united with a much greater degree of flexibility and toughness. It

presents itself under various forms, which may be enumerated under the following heads :—

1. *Interarticular* fibro-cartilages. These are interposed between the moving surfaces of bones, or rather of articular cartilages, in several of the joints. They serve to maintain the apposition of the opposed surfaces in their various motions, to give ease to the gliding movement, and to moderate the effects of great pressure. In the joint of the lower jaw and in that of the clavicle they have the form of round or oval plates, growing thinner towards the centre; in the knee-joint they are curved in form of a sickle, and thinned away towards their concave free edge. In all cases their surfaces are free; while they are fixed by synovial or fibrous membrane at their circumference or extremities. The synovial membrane of the joint is prolonged for a short distance upon these fibro-cartilages, from their attached margin.

2. The articular cavities of bones are sometimes deepened and extended by means of a rim or border of fibro-cartilage. Good examples of these *circumferential* or *marginal* fibro-cartilages are seen in the shoulder and hip-joints, attached round the lip of the articular sockets.

3. *Connecting* fibro-cartilages are such as pass between the adjacent surfaces of bones in joints which do not admit of gliding motion, as at the symphysis of the pubis and between the bodies of the vertebræ. They have the general form of disks, and between the vertebræ are composed of concentric rings of fibrous tissue with cartilage-cells and matrix interposed; the fibrous tissue predominating at the circumference, the cartilaginous tissue increasing towards the centre. The bony surfaces which they connect are usually encrusted with true cartilage.

4. The bony grooves in which tendons of muscles glide are lined with a thin layer of fibro-cartilage. Small nodules of this tissue (*sesamoid fibro-cartilages*) may also be developed in the substance of tendons, of which there is an example in the tendon of the peroneus longus, and also in that of the tibialis posticus, where it passes beneath the head of the astragalus. Lastly, we have an example of the occasional connection of fibro-cartilage with muscle, in the attachment given by it to muscular fibres at the base of the ventricles of the heart.

Fig. 86.

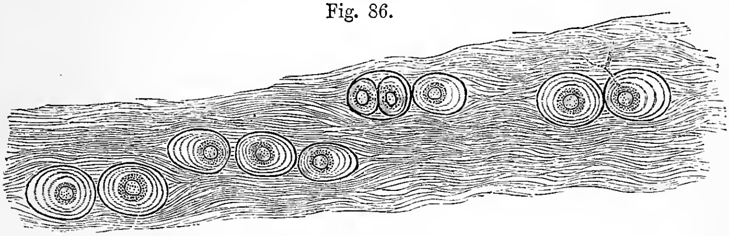

Fig. 86.—White fibro-cartilage from an intervertebral disk (human). Highly magnified (E. A. S.).

The concentric lines around the cells indicate the limits of deposit of successive capsules. One of the cells has a forked process which extends beyond the hyaline area surrounding the cell, amongst the fibres of the general matrix.

Fibro-cartilage appears under the microscope to be made up of wavy fibres, like those of ordinary ligament, with cartilage-cells occupying the place, and often simulating the arrangement, of the tendon-cells. As in elastic fibro-cartilage, the cells are immediately surrounded by a part of the matrix which is free from fibres (fig. 86). As a general rule they resemble the cells of ordinary cartilage, having a rounded shape, although somewhat flattened where the bundles of fibres are closely packed.

In the intervertebral fibro-cartilages, many of the cartilage cells are provided with long and ramified processes that extend far beyond the body of the cell.

The proportion which the fibrous bundles bear to the true cartilage, differs much in different examples of this tissue. In general the fibrous tissue very greatly predominates, and in some cases, as in the inter-articular laminæ of the knee-joint, it constitutes almost the entire structure, but cartilaginous tissue with characteristic cells predominates near the surfaces. In the intervertebral disks the cartilage-corpuscles are, as already stated, more abundant towards the central pulp than near the periphery, but the pulp itself does not in most instances contain cartilage-cells, but a reticulated cell-structure embedded in soft matrix, and probably derived from the cells of the chorda dorsalis of the embryo.

In the healthy state, no blood-vessels penetrate the articular cartilages. Whatever nutrient fluid they require seems to be derived from the vessels of adjoining textures, especially the bone, and to be conveyed through the tissue by imbibition. Towards the circumference of the cartilage, however, underneath the synovial membrane, the synovial vessels form a narrow vascular border round it, which has been named the *circulus articuli vasculosus*.

When the tissue exists in thicker masses, as in the cartilages of the ribs, canals are here and there excavated in its substance, along which vessels are conducted for the nourishment of the parts too distant to receive it from the vessels of the perichondrium. But these canals are few and wide apart, and the vessels do not pass beyond them to ramify in the intermediate mass, which is accordingly quite extravascular.

No nerves have been traced into any of the cartilages, and they are known to be destitute of sensibility.

The matrix of cartilage is chiefly composed of a substance which is converted after long boiling into chondrin. White fibro-cartilage yields gelatine in addition. A certain amount of gelatine is said (by Kühne) also to be yielded by hyaline cartilage.

DEVELOPMENT OF CARTILAGE.

The parts of the embryo which are to become cartilages are made up at first of the common mesodermic cells from which the connective tissues generally originate. After a time the cell-contents become clearer, the nucleus more visible, and the cells, mostly of polygonal outline, appear surrounded by clear lines of pellucid substance, forming as it were a network of bright meshes inclosing them, but in reality consisting of the cohering capsules of the contiguous cells, and constituting all that exists of the matrix at this time.* Glycogen appears at an early period in the protoplasm of cartilage-cells. Rouget found it in the sheep's embryo of two months, both in ossifying cartilage and in the cartilages of the trachea.

The subsequent changes consist in enlargement and multiplication of the cells and development of the intermediate matrix from a substance which is formed around and between them. The process appears to be as follows (fig. 87):—The cartilage cells first divide, a species of capsule being formed round each of the young cells (B), whilst the old one inclosing them becomes blended with the intercellular matrix, and is no longer traceable (C). The new cells, in turn, divide in the same way, so as to make a group of four, each of which is surrounded by its own capsule (D), whilst the capsules of the first descent (secondary) blend with the matrix (E) like their predecessor.

The four cells may each form a succession of capsules and thus become more

* Cartilages, which retain this condition throughout life, have been termed "parenchymatous." An example of this is found in the cartilage of the mouse's ear.

separated from one another, or they may divide again and form a group of eight or more. It is by reason of the cells remaining in contiguity with one another after the division is complete that the groups of corpuscles which are so characteristic of cartilage are produced.

It is doubtful how the capsule is produced; whether excreted by the cell which it afterwards incloses, as held by Kölliker; or formed by conversion of a superficial layer of the protoplasm of the cell-body, as was taught by Max Schultze; or a primarily independent deposit around the cells. However this may be, there is at first no matrix but what is made up of the simple capsules.

Fig. 87.

A B C D E

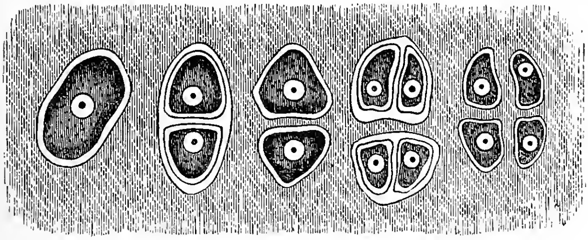

Fig. 87.—Ideal plan of the multiplication of cells of cartilage (Sharpey).

A, cell in its capsule; B, divided into two, each with a capsule; C, primary capsule disappeared, secondary capsules coherent with matrix; D, tertiary division; E, secondary capsules disappeared, tertiary coherent with matrix.

In further growth there is a difference, according as the cells do or do not undergo frequent division. In the latter case a cell becomes surrounded by many concentric capsules formed in succession; that is, the first capsule is expanded, and the others formed each within its expanding predecessor, so that the cartilage comes to consist of scattered cells, each with a concentric system of capsules, which by means of re-agents may be rendered visible in the neighbourhood of the cells, but further off are inseparably blended into a uniform substance. When, on the other hand, the cells have a tendency to frequent subdivision, the new capsules are produced by the new cells, and are included in and finally blend with those which had belonged to the previous cells, as shown by fig. 87.

The matrix, although thus formed of the capsules, usually becomes to all appearance homogeneous; but in sections of cartilage that have been exposed to acids and other re-agents, the contour lines of the capsules round cells and cell-groups may be more or less distinctly brought into view.

The mode in which the division of the cartilage-cell takes place has been carefully studied by Schleicher, and the stages of the process followed in the living tissue (fig. 88). The nuclear membrane first of all disappears, or is converted into filaments of nucleoplasm. These become lost amongst the other filaments which result from the conversion of the nucleoli and other more solid contents of the nucleus. The filaments are at first short and irregular (*a*), and soon take on a stellate arrangement (*b*). After a time they become grouped in a parallel manner in the centre of the nucleus (*c-d*), this phase corresponding with the equatorial stage of division described by Flemming (vide ante, p. 13). The parallel fibres soon divide into two groups, which pass towards the poles of the nucleus. Sometimes the gap between the groups is bridged across for awhile by fine filaments. The two groups of fibres next undergo a gradual process of conversion into the daughter-nuclei (*e-h*).

It will be seen, from the above account, that the division of the *nucleus* of the cartilage cell resembles on the whole that which has been observed in other cells, although all the details of the process have not been distinctly followed. The mode

of division of the *cell-substance* is, however, different, for in place of a constriction appearing and gradually separating the protoplasm into two halves from without in, a partition is formed (*e*), in the middle of the now elongated cell, being produced according to Schleicher, by the accumulation in this situation of some of the filaments, which, as before mentioned (p. 78), occur in the cell-protoplasm. However this may be, the septum, as soon as it is broad enough, is seen in reality to consist of two layers, which are continuous with the capsules of the two daughter cells (*f*).

Fig. 88.

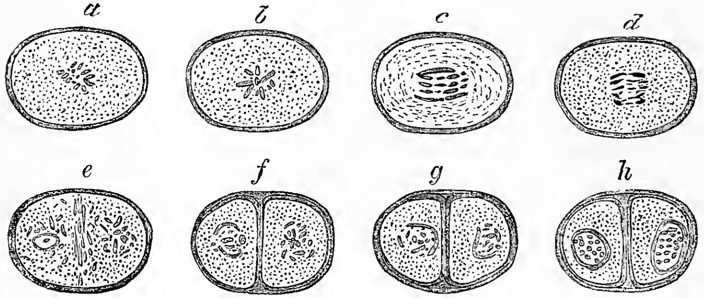

Fig. 88.—Division of a cartilage cell (Schleicher).

a-h, stages of division of a cell, as seen in the living cartilage of the salamander (the connection of the nucleoplasmic filaments could not be made out in the fresh condition). *a*, *b*, stellate phase; *c*, equatorial phase; *d*, commencing separation of the nucleo-plasmic filaments; the further stages of separation are not represented; *e*, filaments fully separated into two groups, and a septum beginning to be formed between them; *f*, septum completed, seen to be double and continuous with capsules of daughter cells; *g*, *h*, further stages in the formation of the daughter nuclei.

In the case of elastic cartilage the matrix is at first hyaline, and the elastic fibres are subsequently produced in it. They appear in the form of fine granules in those parts of the matrix that are in immediate contiguity with the cartilage cells. In the cartilage of the external ear this change occurs about the fifth month of intra-uterine life, commencing in the more central parts, and gradually extending outwards towards the perichondrium.

The mode of development of white fibro-cartilage has not been definitely ascertained.

Nutrition and Regeneration.—The vital changes which occur in cartilage take place very slowly. Its mode of nutrition has been already referred to; it is subject to absorption, and when a portion is absorbed in disease or removed by the knife, it is either not regenerated at all or but very slowly. A wound in cartilage is usually at first healed by connective tissue, which becomes gradually transformed into or gives place to hyaline cartilage. The reappearance of the latter seems, however, to depend upon the presence of the perichondrium, this membrane fulfilling, although perhaps not to so marked an extent, the same functions in the regeneration of cartilage as does the periosteum in the regeneration of bone. Schwalbe found that the cartilage of the rabbit's ear grew only by apposition at its margins and surfaces, and not interstitially; but it is certain that the temporary cartilages grow in the manner last mentioned.

When a cartilage is fractured, as sometimes happens with the rib-cartilages, the broken surfaces become connected, especially at their circumference, by fibrous or dense areolar tissue, and often by a bony clasp.

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BONE OR OSSEOUS TISSUE.

The bones are the principal organs of support, and the passive instruments of locomotion. Connected together in the skeleton, they form a framework of hard material, which affords attachment to the soft parts, maintains them in their due position, and shelters such as are of delicate structure, giving stability to the whole fabric, and preserving its shape; and the different pieces of the skeleton, being joined moveably together, serve also as levers for executing the movements of the body.

While substantially consisting of hard matter, bones in the living body are covered with periosteum and filled with marrow; they are also pervaded by blood-vessels for their nutrition.

Bone has a white colour, with a pink and slightly bluish tint in the living body. Its hardness is well known, but it also possesses a certain degree of toughness and elasticity; the last property is peculiarly well marked in the ribs. Its specific gravity is from 1.87 to 1.97.

Chemical Composition.—Bone consists of an earthy and an animal part, intimately combined together; the former gives hardness and rigidity, the latter tenacity, to the osseous tissue.

The earthy part may be obtained separate by calcination. When bones are burned in an open fire, they first become quite black, like a piece of burnt wood, from the charring of their animal matter; but if the fire be continued with free access of air, this matter is entirely consumed, and they are reduced to a white, brittle, chalk-like substance, still preserving their original shape, but with the loss of about a third of their weight. The earthy constituent, therefore, amounts to about two-thirds of the weight of the bone. It consists principally of phosphate of lime, with about a fifth part of carbonate of lime, and much smaller proportions of fluoride of calcium, chloride of sodium, and magnesian salts.

The animal constituent may be freed from the earthy, by steeping a

bone in diluted hydrochloric acid. By this process the salts of lime are dissolved out, and a tough flexible substance remains, which, like the earthy part, retains the perfect figure of the original bone in its minutest details; so that the two are evidently combined in the most intimate manner. The animal part is often named the cartilage of bone, but improperly, for it differs entirely from cartilage in structure, as well as in physical properties and chemical nature. It is much softer and much more flexible, and, by boiling, it is almost wholly resolved into gelatin. It may accordingly be extracted from bones, in form of a jelly, by boiling them for a considerable time, especially under high pressure.

In the compact substance of a femur that had been long buried, Aeby found only 16·5 per cent. of animal matter.

The fluoride of calcium is found in larger quantity in fossil than in recent bones.

MINUTE STRUCTURE OF BONE.

On sawing up a bone, it will be seen that it is in some parts dense and close in texture, appearing like ivory; in others open and reticular: and anatomists accordingly distinguish two forms of osseous tissue, viz., the *compact*, and the *spongy* or *cancellated*. On closer examination, however, especially with the aid of a magnifying glass, it will be found that the bony matter is everywhere porous in a greater or less degree, and that the difference between the two varieties of tissue depends on the different amount of solid matter compared with the size and number of the open spaces in each; the cavities being very small in the compact parts of the bone, with much dense matter between them; whilst in the cancellated texture the spaces are large, and the intervening bony partitions thin and slender. There is, accordingly, no abrupt limit between the two,—they pass into one another by degrees, the cavities of the compact tissue widening out, and the reticulations of the cancellated becoming closer as they approach the parts where the transition between the two takes place.

In all bones, the part next the surface consists of compact substance, which forms an outer shell or crust, whilst the spongy texture is contained within. In a long bone, the large round ends are made up of spongy tissue, with only a thin coating of compact substance; in the hollow shaft, on the other hand, the spongy texture is scanty, and the sides are chiefly formed of compact bone, which increases in thickness from the extremities towards the middle, at which point the girth of the bone is least, and the strain on it greatest. In tabular bones, such as those of the skull, the compact tissue forms two plates, or tables, as they are called, inclosing between them the spongy texture, which in such bones is usually named *diploë*. The short bones, like the ends of the long, are spongy throughout, save at their surface, where there is a thin crust of compact substance. In the complex or mixed bones, such as the vertebræ, the two substances have the same general relation to each other; but the relative amount of each in different parts, as well as their special arrangement in particular instances, is very various.

On close inspection the cancellated texture of bone is seen to be formed of slender bars or spicula and thin lamellæ, which meet together and join in a reticular manner, producing an open structure which has been compared to lattice-work (*cancelli*), and hence the name usually

applied to it. In this way considerable strength is attained without undue weight, and it may usually be observed that the strongest laminæ run through the structure in those directions in which the bone has naturally to sustain the greatest pressure. The open spaces or areolæ of the bony network communicate freely together; in the fresh state they contain marrow or blood-vessels, and give support to these soft parts.

Fig. 89.

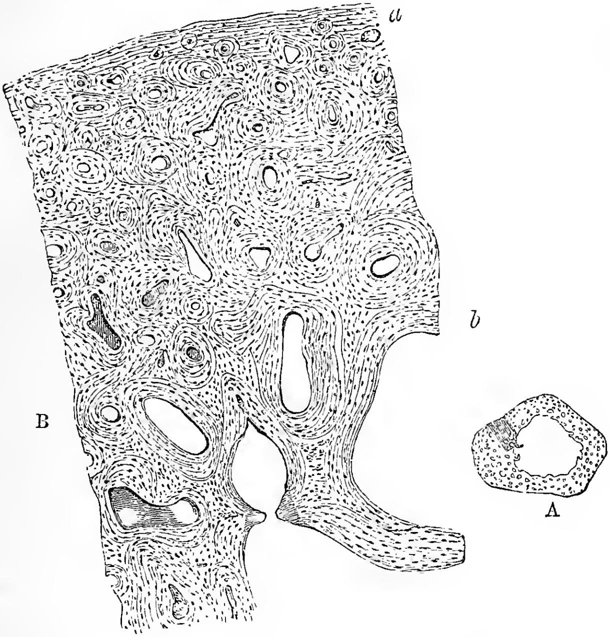

Fig. 89.—A, Transverse section of a bone (ulna) deprived of its earth by acid (Sharpey).

The openings of the Haversian canals are seen. Natural size. A small portion is shaded to indicate the part magnified in Fig. B.

B, Part of the Section A, magnified 20 diameters.

The lines indicating the concentric lamellæ are seen, and among them the lacunæ appear as little dark specks.

Haversian canals.—The compact tissue is also full of holes; these, which are very small, are best seen by breaking across the shaft of a long bone near its middle and examining it with a common magnifying glass. Numerous little round apertures (fig. 89 A) may then be seen on the broken surface, which are the openings of short longitudinal passages running in the compact substance, and named the *Haversian canals*, after Clopton Havers, an English physician and writer of the seventeenth century, who more especially called attention to them. Blood-vessels run in these canals, and the widest of them also contain marrow. They are from $\frac{1}{1000}$th to $\frac{1}{200}$th of an inch in diameter: there are some no more than $\frac{1}{2000}$th, but these are rare; the medium size is

about $\frac{1}{500}$th. The widest are met with nearest the medullary cavity, and the narrower towards the circumference of the bone. They are quite short, as may be seen in a longitudinal section, oblique communications connecting them freely both longitudinally and laterally. Those which are next the circumference of the bone, open by minute pores on its external surface, and the innermost ones open widely into the medullary cavity; so that these short channels collectively form a sort of irregular network of tubes running through the compact tissue, in which the vessels of that tissue are lodged, and through the medium of which these vessels communicate together, not only along the length of the bone, but from its surface to the interior through the thickness of the shaft. The canals of the compact tissue in the other classes of bones have the same general characters, and for the most part run parallel to the surface.

Lamellæ.—On viewing a thin transverse section of a long bone with a microscope of moderate power, especially after the earthy part has been removed by acid (fig. 89 B; fig. 95), the opening of each Haversian canal appears to be surrounded by a series of concentric rings. This appearance is occasioned by the transverse sections of concentric *lamellæ* which surround the canals. The rings are not all complete, for here and there one may be seen ending between two others. In some of the sets, the rings are nearly circular, in others oval,—differences which seem mostly to depend on the direction in which the canal happens to be cut: the aperture too, may be in the centre, or more or less to one side, and in the latter case the rings are usually narrower and closer together on the side towards which the aperture deviates. Again, some of the apertures are much lengthened or angular in shape, and the lamellæ surrounding them have a corresponding disposition. Besides the lamellæ surrounding the Haversian canals, there are others disposed conformably with the circumference of the bone (fig. 89 B, *a*), most of these are near the surface, but others run between the Haversian sets, by which they are interrupted in many places (fig. 95). Lastly, in various parts of the section, lines are seen which indicate lamellæ, differing in direction from both of the above-mentioned orders.

The appearance in a longitudinal section of the bone is in harmony with the account above given: the sections of the lamellæ are seen as straight and parallel lines, running in the longitudinal direction of the bone, except when the section happens to have passed directly or slantingly across a canal: for wherever this occurs there is seen, as in a transverse section, a series of rings, generally oval and much lengthened on account of the obliquity of the section.

The cancellated texture has essentially the same lamellar structure. The slender bony walls of its little cavities or areolæ are made up of superimposed lamellæ, like those of the Haversian canals, only they have fewer lamellæ in proportion to the width of the cavities which they surround; and, indeed, the relative amount of solid matter and open space constitutes, as already said, the only difference between the two forms of bony tissue: the intimate structure of the solid substance and the manner of its disposition round the cavities being essentially the same in both.

Lacunæ and canaliculi.—All over the section numerous little dark specks are seen among the lamellæ. These were named the "osseous corpuscles;" but as it is now known that they are in reality minute

cavities existing in the bony substance, the name of *lacunæ* has since been more fittingly applied to them. To see the lacunæ properly, however, sections of unsoftened bones must be prepared and ground very thin, and a magnifying power of from 200 to 300 must be employed. Such a section, viewed with transmitted light, has the appearance represented in fig. 90. The openings of the Haversian canals are seen with their encircling lamellæ, and among these the lacunæ, which are mostly ranged in a corresponding order, appear as black or dark brown and nearly opaque oblong spots, with fine dark lines extending from them and causing them to look not unlike little black insects. The dark appearance is due to the fact that the little cavities have become filled with air in the dry bone, and when the same section is seen against a dark ground, with the light falling on it (as we usually view an opaque object), the little bodies and lines appear quite white, like figures drawn with chalk on a slate, and the intermediate substance, being transparent, now appears dark.

Fig. 90.

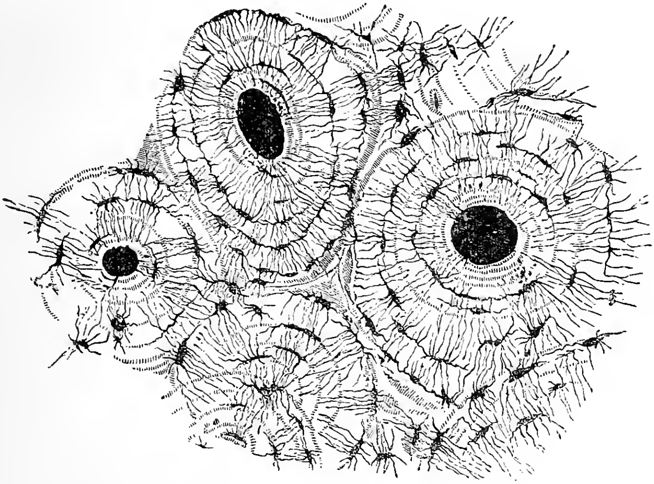

Fig. 90.—Transverse section of compact tissue (of humerus) magnified about 150 diameters (Sharpey).

Three of the Haversian canals are seen, with their concentric rings; also the lacunæ, with the canaliculi extending from them across the direction of the lamellæ. The Haversian apertures had become filled with débris in grinding down the section, and therefore appear black in the figure, which represents the object as viewed with transmitted light.

The lacunæ, as already stated, are minute recesses in the bone, and the lines extending from them are fine pores or tubes named *canaliculi*, which issue from their cavity. The lacunæ present some variety of figure, but in such a section as that represented they for the most part appear irregularly fusiform, and lie nearly in the same direction as the lamellæ between which they are situated; or, to speak more correctly, they are flattened and extended conformably with the lamellæ; for when the bone is cut longitudinally, their sections still appear fusiform and are still more lengthened out in the direction of the lamellæ.

The canaliculi, on the other hand, pass across the lamellæ, and they communicate with those proceeding from the next range of lacunæ, so as to connect the little cavities with each other; and thus since the canaliculi of the most central range open into the Haversian canal, a system of continuous passages is established by these minute tubes and their lacunæ, along which fluids may be conducted from the Haversian canal through its series of surrounding lamellæ; indeed, it seems probable that a chief purpose of these minute passages is to allow nutrient matter to be conveyed from the vascular Haversian canals through the mass of hard bone which lies around and between them. In like manner the canaliculi open into the great medullary canal, and into the cavities of the cancellated texture; for in the thin bony parietes of these cavities lacunæ are also contained; they exist, indeed, in all parts of the bony tissue. The canaliculi which radiate outwards from the lacunæ near the periphery of the Haversian systems do not as a rule communicate with those of the neighbouring Haversian system, but bend round and are joined to one another.

Cells of bone.—As first shown by Virchow, each lacuna is occupied by a flattened nucleated cell, which sends branches along the canaliculi; and later observers (Rouget, Neumann,) have been able to detach the

Fig. 91.

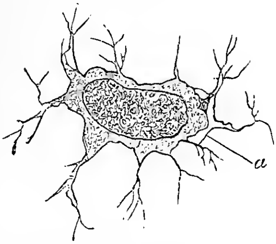

Fig. 91. A BONE-CELL ISOLATED AND HIGHLY MAGNIFIED (after Joseph).

a, proper wall of the lacuna, shown at a part where the corpuscle has shrunk away from it.

proper wall of the lacuna and its appertaining canaliculi after decalcification, and to obtain it separate with its included corpuscle. It can scarcely be doubted that the protoplasm of the nucleated corpuscle takes an important share in the nutritive process in bone, and very probably serves both to modify the nutritive fluid supplied from the blood and to further its distribution through the lacunar and canalicular system of the bony tissue. Virchow showed that the corpuscles of bone are homologous with those of connective tissue: to this it may be added that the enclosing lacunæ and canaliculi are to be looked upon as corresponding to the cell-spaces of that tissue.

Apertures and decussating fibres of the lamellæ.—With a little pains, thin films may be peeled off in a longitudinal direction from a piece of bone that has been softened in acid. These for the most part consist of several lamellæ, as may be seen at the edge, where the different layers are usually torn unequally, and some extend farther than others. Examined in this way, under the microscope, the lamellæ are seen to be perforated with fine apertures placed at very short distances apart. These apertures were described by Deutsch;* they appear to be the transverse sections of the canaliculi already described, and their relative distance and position accord sufficiently with this explanation. According to this view, therefore, the canaliculi might (in a certain sense) be conceived to result from the apposition of a series of perforated plates, the apertures

* De Penitiori Ossium Structurâ. Wratisl. 1834, p. 17, Fig. 6.

of each plate corresponding to those of the plates contiguous with it; or they might be compared to holes bored to some depth in a straight or crooked direction through the leaves of a book, in which case it is plain that the perforations of the adjoining leaves would correspond; it being understood, however, that the passages thus formed are most likely bounded by proper parietes. The apertures now referred to must be distinguished from larger holes seen in some lamellæ, which give passage to the perforating fibres to be mentioned further on.

But the lamellæ have a further structure. To see this, the thinnest part of a detached shred or film must be examined, as shown in figs. 92 and 94; it will then appear plainly that they are largely made up of transparent fibres, decussating with each other in the form of an exceedingly fine network. In the Haversian systems these decussating fibres cross one another in different lamellæ at right angles (v. Ebner), but in most other situations at more or less acute angles, and they are united here and there by obliquely passing fibres, so that they cannot be teased out from one another; but at the torn edge of the lamella they may often be seen separate for a little way, standing out like the threads of a fringe. Most generally they are straight, as represented in

Fig. 92.—Thin layer peeled off from a softened bone, as it appears under a magnifying power of 400 diameters (Sharpey).

This figure, which is intended to represent the reticular structure of a lamella, gives a better idea of the object when held rather farther off than usual from the eye.

Fig. 92.

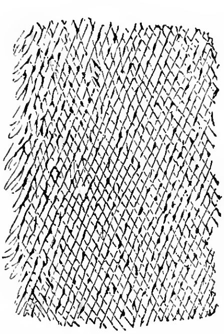

fig. 92; but they are not always so, for in some parts they assume a curvilinear direction (fig. 94). Acetic or hydrochloric acid causes these fibres to swell up and become indistinct, like the white fibres of connective tissue; care must therefore be taken in their examination that the remains of the decalcifying acid be removed from the tissue, by maceration in water or in solutions of certain salts. Moreover, the fibro-reticular structure is not equally distinct in all parts; for in some places it is less decidedly marked, as if the fibrillation were incompletely developed.

The decussating fibres which constitute the lamellæ were discovered by Sharpey, and their constant presence was taught by him for a long time before they were admitted by other histologists. It has lately been shown by v. Ebner that the decussating fibres of Sharpey are in reality themselves composed of exquisitely fine fibrils, so that they correspond with bundles of white connective tissue fibres rather than with single fibres. Like the connective tissue fibrils these of the bone are doubly refracting, and they are said not to be calcified, the deposit of calcareous matter being confined to the matrix in which they are embedded. They appear to be united into the lamellæ by a matrix or ground-substance, and according to v. Ebner take different directions in successive lamellæ, so as to produce a granular or a striated appearance according as they happen to be cut transversely or longitudinally (fig. 93).

In thin sections of bone, the concentric lines or rather bands which represent the cut edges of the lamellæ show the section of the decussating fibres as round or angular dots, themselves punctated, which lie embedded in the homogeneous ground-substance (fig. 93, *b*). The lamellæ are separated from one another by the lacunæ which lie between them, where these are absent they are joined

together by the ground-substance; they may also be united by occasional bundles of fibres passing obliquely from one lamella to the other.

Fig. 93.

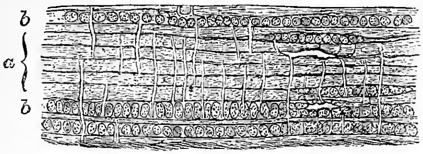

Fig. 93.—Small part of a longitudinal section of decalcified tibia. Highly magnified (after v. Ebner).

a, series of six lamellæ which are cut for the most part in the direction of the fibrils, so that they appear longitudinally striated; *b*, *b*, lamellæ, the fibrils of which are cut across; the arrangement of the fibrils into bundles is indicated. Two or three lacunæ are seen lying between the lamellæ, their canaliculi piercing the lamellæ.

Perforating fibres.—It was further shown by Sharpey that in many instances the lamellæ are perforated by fibres, which pass through them in a perpendicular, or oblique direction, and, as it were, bolt them together. These perforating fibres may be seen, with the aid of the microscope, in a thin transverse slice of a decalcified cylindrical or cranial bone, on pulling asunder the sections of the lamellæ (as in fig. 96). In this way some lamellæ will generally be observed with fibrous processes attached to them (fig. 96, *b*) of various lengths, and usually tapering and pointed at their free extremities, but sometimes truncated—probably from having been divided by the knife. These fibres have obviously been drawn out from the adjacent lamellæ, through several of which they must have penetrated. Sometimes, indeed, indications of perforations may be recognised in the part of the section of bone from which the

Fig. 94.

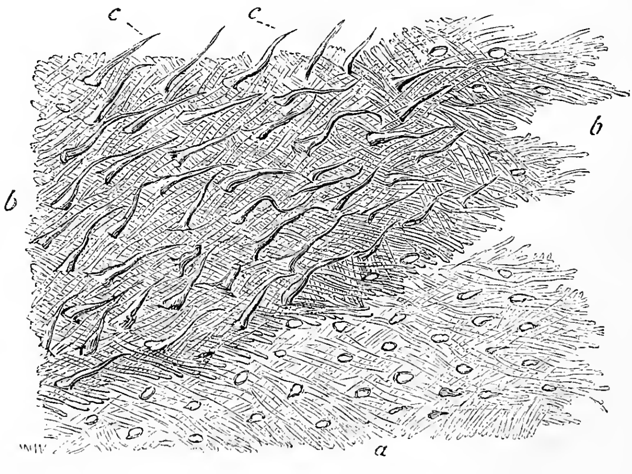

Fig. 94.—Lamellæ torn off from a decalcified human parietal bone at some depth from the surface (Sharpey).

a, lamellæ, showing decussating fibres; *b*, *b*, thicker part, where several lamellæ are superposed; *c*, *c*, perforating fibres. Apertures through which perforating fibres had passed, are seen especially in the lower part, *a*, *a*, of the figure. Magnitude as seen under a power of 200, but not drawn to a scale (from a drawing by Allen Thomson).

fibres have been pulled out (fig. 96, *c*). The processes in question are thus, so to speak, viewed in profile; but they may frequently also be seen on the flat surface of detached lamellæ (fig. 94), projecting like nails driven perpendicularly.

The perforating fibres are, like the decussating fibres, for the most part bundles of fibrils which agree in character with those of the white fibrous tissue; but some, as shown by H. Müller, are of the nature of elastic tissue (fig. 95, *e*). In some parts thev escape calcification,

Fig. 95.

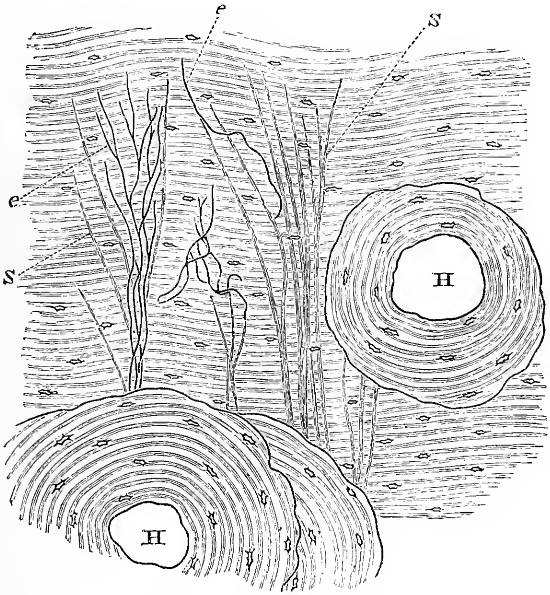

Fig. 95.—Transverse section of decalcified human tibia, from near the surface of the shaft (E. A. S.).

H, H, Haversian canals, with their systems of concentric lamellæ; in all the rest of the figure the lamellæ are circumferential.

s, ordinary perforating fibres of Sharpey; *e*, *e*, elastic perforating fibres. Drawn under a power of about 150 diameters.

and thus, as they shrink in drying, leave tubes or channels in the dry bone, generally leading from the surface inwardly; but these uncalcified fibres are by no means frequent. The perforating fibres are often connected with the periosteum, as is the case with most of those which penetrate the external table of the cranial bones; but in cross sections of cylindrical bones they often appear to spring with their broad ends from the deeper lamellæ (with the fibres of which they may be directly continuous), and especially from those near the circumference of a Haversian system, and taper outwards into fine points, which do not reach the periosteum (fig. 95); although without doubt they must, like the bony layers in which they occur, have been formed by subperiosteal ossification. They are rarely if ever found in the concentric

systems of Haversian lamellæ. Perforating fibres exist abundantly in the *crusta petrosa* of the teeth (Sharpey).

Where tendons or ligaments are inserted into bone, the fibre-bundles of the tendon are continued into the bone as perforating fibres, so that the attachment of tendon to bone is thus rendered very intimate. Some of the bundles of white fibres of the periosteum may also, as above mentioned, pass into the bone as perforating fibres, and the same is the case with the elastic fibres.

Fig. 96.

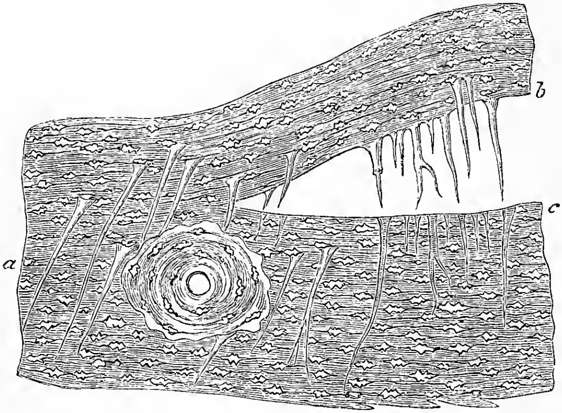

Fig. 96.—Magnified view of a perpendicular section through the external table of a human parietal bone, decalcified (H. Müller).

At *a*, perforating fibres in their natural situation ; at *b*, others drawn out by separation of the lamellæ ; at *c*, the holes or sockets out of which they have been drawn (H. Müller).

The animal basis of bone is made up essentially, as we have seen, of lamellæ composed of fine decussating or reticular fibril-bundles embedded in a ground-substance ; but interposed among these lamellæ, layers are here and there met with of a different character, having a granular aspect, with the lacunæ very conspicuous and regularly arranged, and sometimes appearing as if surrounded by faintly defined areolæ. These generally incomplete layers are often bounded by a scalloped border, as if made up of confluent round or oval bodies ; this is indicated also by the occasional occurrence of oval or flattened spheroidal bodies singly or in small groups near the border of the layers, each with a lacuna in the centre. In some parts the granular substance is obscurely fibrous, and transitions may be observed to the well-marked reticular laminæ. The layers described appear principally to occur near the surface of the compact tissue, and at the circumference of many of the systems of concentric Haversian lamellæ.

Irregular layers of rounded bodies, apparently solid and without central cavity, are also sometimes seen, and are well represented in figure 97. These layers are met with chiefly near the surface of the shaft of long bones, lying among the circumferential laminæ, and apparently forming only part of a circuit. They can occasionally be recognised in a transverse section as short curvilinear bands of peculiar aspect, broader in the middle and thinning away at the ends, appearing here and there between the cut edges of two ordinary circumferential laminæ.

Finally, spaces are occasionally seen in a section of bone, which are characterized by an eroded outline, but in some cases they may be partially filled up by concentric lamellæ. These were named " Haversian spaces " by Tomes and de Morgan, and they are interpolated or intruded amongst the regular Haversian systems, some of which may have been cut in upon in the excavation of the

space. It was further noticed by Tomes and de Morgan that the spaces in question may sometimes be seen being filled up at one part by the deposition of lamellæ, whilst they are extending themselves by absorption at another. The Haversian spaces are most numerous in young and growing bones, but they occur also after growth is completed.

The three appearances above mentioned are due to the peculiar manner in which the absorption of bone occurs ; for it is effected, as will presently be described, by

Fig. 97

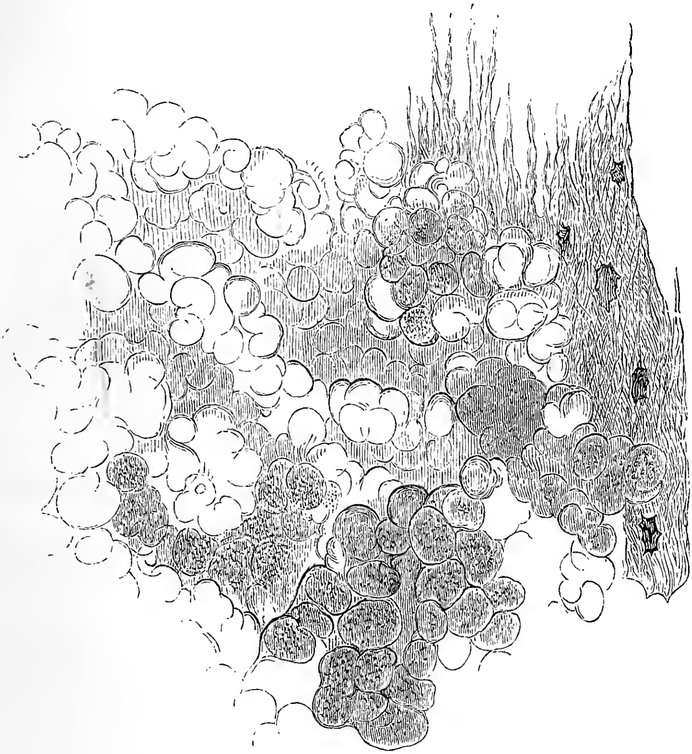

Fig. 97.—Portion of a nodulated layer of bone-tissue from near the surface of the shaft of a decalcified humerus (Sharpey).

At one side shreds of fibrous lamellæ are seen in the figure. Magnified 300 diameters. From a drawing by Allen Thomson.

the agency of large multinucleated cells, which excavate little hemispherical pits in the osseous tissue. If the process of absorption should cease and should be succeeded by a re-deposition of osseous substance, the new osseous matter filling up the hollows of the absorbed surface exhibits, when it is detached, a raised impression corresponding with the hollows into which it fitted.

In young bones the lamellar character is far less distinct than in adult bones, the tissue being constituted chiefly of bundles of fibres which interlace in every direction in the ground substance ; in this reticular form of osseous tissue the lacunæ are both more numerous and irregular than in lamellated bone.

When, as is often the case, tendons become ossified, little but a calcification of the ground substance of the tendon occurs, so that, after decalcifying, the tendinous structure again becomes manifest.

The exact knowledge we possess of the minute structure of osseous tissue is largely the result of the careful and laborious research of the late Professor Sharpey, whose account, published in the fifth edition of this work in 1845, has needed no erasure, and but little addition, even to the present day. His labours in this field have been to a certain extent recognized in the adoption of the name "fibres of Sharpey" for the perforating fibres discovered by him, but it is only now, after the lapse of many years, that the facts which he demonstrated are becoming understood and their significance appreciated by histologists.

THE PERIOSTEUM.

The **periosteum**, as already stated, is a fibrous membrane which covers the bones externally. It adheres to them very firmly, and invests every part of their surface, except where they are covered with cartilage.

It is composed of two layers; the outer, consisting chiefly of white fibres, and containing occasional fat-cells, is the means of supporting numerous blood-vessels destined for the bone, which ramify in the membrane, and at length send their minute branches into the Haversian canals of the compact substance, accompanied by processes of filamentous tissue derived from, or at least continuous with, the periosteum. The inner layer is largely made up of elastic fibres, frequently in several distinct strata. Between it, however, and the proper osseous tissue there is a fibrous stratum containing in the young bone a number of granular corpuscles (osteoblasts), while in the adult bone these have become flattened out into an epithelioid layer covering the osseous substance, and are in many places separated by a cleft-like space (serving probably for the passage of lymph) from the rest of the periosteum (Schwalbe).

By treating the membrane with nitrate of silver, lymphatics are discovered in it accompanying the blood-vessels in the outer layer; and, as in other aponeurotic structures, extensive epithelioid markings, covering a great part of the surface, are brought into view.

Fine nerves spread out in the periosteum; they are chiefly associated with the arteries, and for the most part destined for the subjacent bone; but some are for the membrane itself, and some of these end in Pacinian corpuscles.

The chief use of the periosteum is to support the vessels going to the bone, and afford them a bed in which they may subdivide into fine branches, and so enter the dense tissue at numerous points. Hence, when the periosteum is stripped off at any part, there is great risk that the denuded portion of the bone will die and exfoliate. The periosteum also contributes to give firmer hold to the tendons and ligaments where they are fixed to bones. Its relation to the growth and renewal of bone will be referred to later on.

THE MARROW.

The **marrow** (*medulla ossium*) is lodged in the interior of the bones; it fills up the hollow shaft of long bones and occupies the cavities of the cancellated structure; it extends also into the Haversian canals—at least into the larger ones—along with the vessels. A fine layer of a highly vascular areolar tissue lines the medullary canal, as well as the smaller cavities which contain marrow; this has been named the medullary membrane, internal periosteum, or endosteum; but it cannot be detached as a continuous membrane. Its vessels partly supply the contiguous osseous substance, and partly proceed to the clusters of adipose

vesicles, among which there is but very little connective tissue, in consequence perhaps of their being contained and supported by bone.

The marrow differs considerably in different situations. Within the shaft of the long bones it is of the character of ordinary adipose tissue, but the fat-cells are supported by a kind of retiform tissue, and between them elements occur similar to those immediately to be mentioned in the red marrow. In short bones, and in the cancellated ends of long bones, but especially in the cranial diplöe, the bodies of the vertebræ, the sternum, and the ribs, the marrow is red or reddish in colour, of more fluid consistence, and with very few fat-cells. While, however, the fat-cells are scanty in the red-coloured marrow, it contains numerous roundish nucleated cells—the proper *marrow-cells* of Kölliker (fig. 98, *e*—*i*). These in general appearance resemble the pale corpuscles of the blood, but are larger, with a clearer protoplasm and a relatively larger nucleus. Like the pale corpuscles, they exhibit amœboid movements. Amongst them are smaller cells which present a reddish colour, and resemble in appearance the primitive nucleated corpuscles of the embryo (fig. 98, *j*—*t*); these are the cells which have been described as representing transitional forms between the proper marrow-cells and red blood-disks (vide ante, p. 37).

Fig. 98.

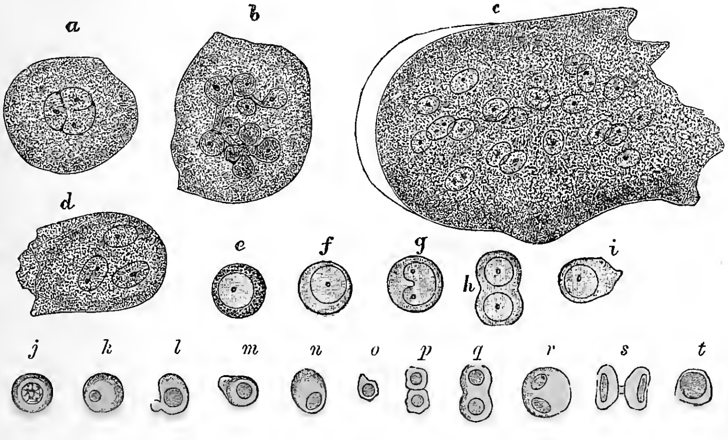

Fig. 98.—Cells of the red marrow of the guinea-pig. Highly magnified. (E. A. S.)

a, a large cell the nucleus of which appears to be partly divided into three by constrictions; *b*, a cell the enlarged nucleus of which shows an appearance of being constricted into a number of smaller nuclei; *c*, a so-called giant-cell or myeloplaxe with many nuclei; *d*, a smaller myeloplaxe with three nuclei; *e*—*i*, proper cells of the marrow; *j*—*t*, various forms of coloured nucleated cells.

Other cells have occasionally been noticed containing one or more red corpuscles in their interior: whether these have been developed *in situ* in a manner similar to that previously described in connective tissue corpuscles of the young animal, or have been taken into the interior of an amœboid cell, there to be transformed into pigment granules, is not certainly known. Cells containing reddish pigment granules are, however, not uncommon. There further occur in the marrow, especially in the neighbourhood of the osseous substance, large multi-nucleated proto-

plasmic masses (*myeloplaxes*, Robin (fig. 98, *a—d*)), which, as pointed out by Kölliker, appear to be more especially concerned with the process of absorption of bone, under which head they will subsequently be further alluded to. The myeloplaxes vary much in size, but are always larger than the proper marrow-cells. Their nucleus is not always multiple, but when single it is usually enlarged, and presents indications of division (fig. 98, *a*) ; it may even be so constricted as to exhibit an irregularly moniliform appearance (fig. 98, *b*).

THE BLOOD-VESSELS AND LYMPHATICS OF BONE

Blood-vessels.—The bones are well supplied with blood-vessels. A network of periosteal vessels covers their outer surface ; fine vessels run from this through all parts of the compact tissue in the Haversian canals ; others penetrate to the cavities of the spongy part, in which they ramify ; and a considerable artery goes to the marrow in the central part of the bone. In the long bones this *medullary artery*, often, but improperly, called " the nutritious artery," passes into the medullary canal, near the middle of the shaft, by a hole running obliquely through the compact substance. The vessel, which is accompanied by one or two veins, then sends branches upwards and downwards to the marrow and medullary membrane in the central cavity and the adjoining Haversian canals ; from these branches capillaries pass radially towards the periphery. The comparatively narrow arterial capillaries pass suddenly into the wide venous ones, so that the current of blood must be considerably retarded both in these and in the large thin-walled veins.

The ramifications of the medullary artery anastomose with the arteries of the compact and cancellated structure ; indeed, there is a free communication between the finest branches of all the vessels which proceed to the bone, and there is no strictly defined limit between the parts

Fig. 99.

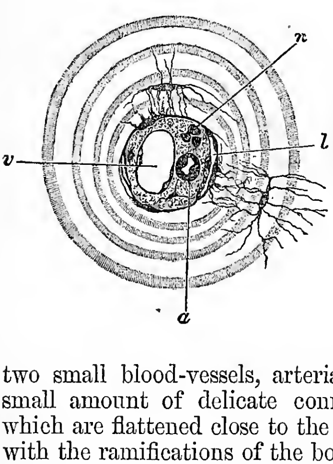

Fig. 99.—Section of a Haversian canal, showing its contents. Highly magnified. (E.A.S.)

a, small arterial capillary vessel ; *v*, large venous capillary ; *n*, pale nerve-fibres cut across ; *l*, cleft-like lymphatic vessel : one of the cells forming its wall communicates by fine branches with the branches of a bone-corpuscle. The substance in which the vessels run is connective tissue with ramified cells ; its finely granular appearance is probably due to the cross section of fine fibrils.

supplied by each. In the thigh bone there are frequently two medullary arteries entering at different points.

Most of the Haversian canals contain two small blood-vessels, arterial and venous (fig. 99), together with a small amount of delicate connective tissue containing branched cells which are flattened close to the bone, and communicate by their branches with the ramifications of the bone-corpuscles.

The veins of the cancellated texture are peculiar and deserve special notice. Their arrangement is best known in the bones of the skull, where, being lodged in the diplöe or spongy texture between the outer and inner compact tables, they have received the name of the diplöic veins. They are large and numerous,

and run separately from the arteries in canals formed in the cancellated structure, the sides of which are constructed of a thin lamella of bone, perforated here and there for the admission of branches from the adjoining cancelli. Being thus inclosed and supported by the hard structure, the veins have exceedingly thin coats. They issue from the bone by special apertures of large size. A similar arrangement is seen in the bodies of the vertebræ, from whence the veins come out by large openings on the posterior surface. In the long bones numerous apertures may be seen at the ends, near the articular surfaces; some of these give passage to arteries, but the greater number, as well as the larger of them, are for the veins of the cancellated texture, which run separately from the arteries.

According to Hoyer and Rindfleisch the venous capillaries and veins of the red marrow have incomplete walls, or rather are channels bounded only by the medullary parenchyma, so that the blood-corpuscles which are being formed from marrow-cells can readily get into the circulation. Langer, on the other hand, found the vascular system of the marrow to be a closed one. That the channels in which the blood flows are bounded by elongated cells, similar to those of capillaries in other situations, it is easy, Rindfleisch notwithstanding, to see, but at the same time it must be admitted that the extreme ease with which these cells separate from one another betokens the lack of a complete union between them, and a greatly increased permeability of the vascular wall in consequence.

The blood coming from the marrow possesses a large number of pale corpuscles, as well as nucleated red corpuscles.

Lymphatics.—In addition to the lymphatics in the periosteum (which have already been mentioned), there are others in the Haversian canals accompanying the vessels (fig. 98, *l*), and often partially or wholly enclosing them (perivascular). The lymph or plasma of the blood is enabled to penetrate the hard bony substance by means of the lacunæ and communicating canaliculi, which appear to bear the same relation to the lymphatics as do the cell-spaces of ordinary connective tissue to the lymphatics of that tissue.

The fine **nerves** which may be seen entering the bones along with the arteries are probably chiefly destined for those vessels; it is not known whether any end in the bony tissue itself.

As far as can be judged from observations on man and experiments on the lower animals, the bones, as well as their investing periosteum, are scarcely if at all sensible in the healthy condition, although they are painfully so when inflamed.

FORMATION AND GROWTH OF BONE.

The foundation of the skeleton is laid at a very early period; for, among the parts that appear soonest in the embryo, we distinguish the rudiments of the vertebræ and base of the skull, which afterwards form the great median column to which the other parts of the bony fabric are appended. But it is by their outward form and situation only, that the parts representing the future bones are then to be recognised; for at that early period they do not differ materially in substance from the other structures of the embryo, being made up of mesodermic cells, with a small amount of intercellular substance. Very soon, however, they become cartilaginous, and ossification in due time beginning in the cartilage and continuing to spread from one or from several points, the bony tissue becomes gradually formed.

But, while it is true with respect to the bones generally that their ossification commences in cartilage, it is not so in every instance. The tabular bones forming the roof of the skull may be adduced as a decided example to the contrary; in these the ossification goes on in connective

tissue altogether unconnected with any cartilage ; and even in the long bones, in which ossification undoubtedly commences and to a certain extent proceeds in cartilage, it will be afterwards shown that there is much less of the increment of the bone really owing to that mode of ossification than was at one time generally believed. It is necessary, therefore, to distinguish two species or modes of ossification, which for the sake of brevity may be called the *intramembranous* and the *intracartilaginous*.

INTRAMEMBRANOUS OSSIFICATION: OSSIFICATION IN CONNECTIVE TISSUE.

The tabular bones of the cranium, as already said, afford an example of this mode of ossification. The base of the skull in the embryo is cartilaginous ; but in the roof, that is to say, the part comprehending the parietal, the frontal, and a certain portion of the occipital bones, we find (except where there happen to be commencing muscular fibres) only the integuments, the dura mater, and an intermediate layer, in which the ossification proceeds.

The commencing ossification of the parietal bone, which may be selected as an example, appears to the naked eye in the form of a network in which the little bars or spicula of bone run in various directions, and meet each other at short distances. By-and-by the ossified part, becoming extended, gets thicker and closer in texture, especially towards the centre, and the larger bony spicula which now appear, run out in

Fig. 100.

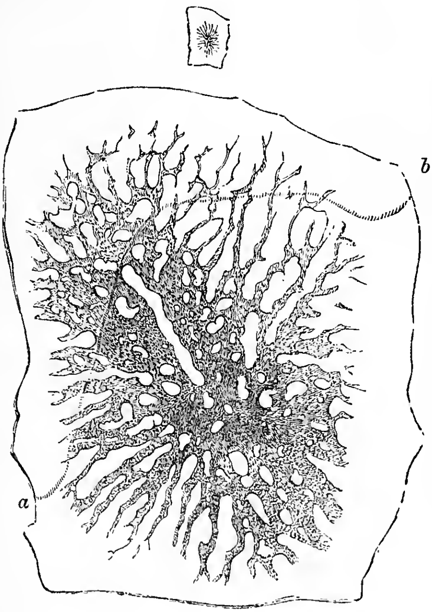

Fig. 100.—PARIETAL BONE OF AN EMBRYO SHEEP. SIZE OF THE EMBRYO, $2\frac{1}{2}$ INCHES. (Sharpey.)

The small upper figure represents the bone of the natural size, the larger figure is magnified about 12 diameters. The curved line, *a*, *b*, marks the height to which the subjacent cartilaginous lamella extended. A few insulated particles of bone are seen near the circumference, an appearance which is quite common at this stage.

radiating lines to the circumference. The ossification continues thus to spread and consolidate until the parietal meets the neighbouring bones, with which it is at length united by sutures.

Fig. 100 represents the parietal bone of an embryo sheep about two inches and a half long, and shows the character of the ossification as it appears when the object is magnified about twelve diameters. The bone is formed in membrane as in the human fœtus, but a thin plate of cartilage rises up on its inside from the base of the skull. The ossification, however, is decidedly unconnected with the cartilage, and goes on in a membrane lying outside of it.

When further examined with a higher magnifying power, the tissue or membrane in which the ossification is proceeding, appears to be made up of fibres and granular corpuscles, with a ground substance between, and, in point of structure, may not unaptly be compared to connective tissue in a certain stage of development. The corpuscles are large and angular, and they are densely packed all over the area of ossification, covering the bony spicula, and filling up their interstices.

On observing more closely the points of the growing osseous rays at the circumference of the bone, where they shoot out into the soft tissue, it will be seen that the portion of them already calcified is granular and rather dark in appearance (fig. 101), but that this character is gradually

Fig. 101.

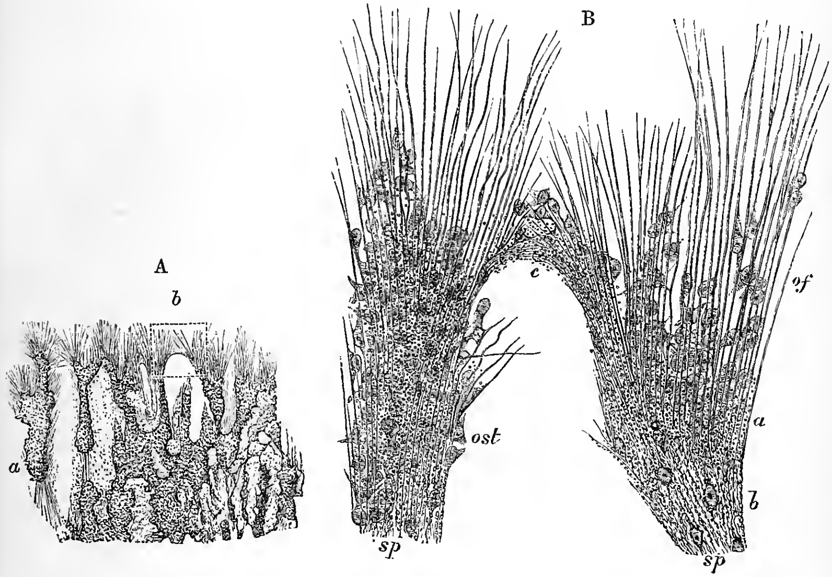

Fig. 101.—Part of the developing parietal bone of a fœtal cat ($1\frac{1}{2}$ inch long). (From drawings by Mr. J. Lawrence.) (E.A.S.)

A, a piece of the growing edge slightly magnified, showing the bony spicules terminated by bunches of osteogenic fibres; *a*, an isolated bony spicule united to the main part of the ossification by a bundle of osteogenic fibres.

B, the part marked *b* of the smaller figure, highly magnified; *sp*, bony spicules, with some of the osteoblasts imbedded in them, producing the lacunæ; *ost*, osteoblasts partly imbedded in the newly formed bone; *of*, osteogenic fibres prolonging the spicules, with osteoblasts between them and applied to them; *a*, granules of calcareous deposit between the osteogenic fibres; at *b* the granules have become blended, and the matrix is clearer; at *c* a continuity is established between the two adjacent spicules.

lost as they are traced further outwards in the membrane, in which they are prolonged for a little way in form of soft and pliant bundles of transparent fibres (fig. 101, B, *of*).

These are termed *osteogenic fibres,* the soft transparent matter of which they are composed being known as osteogenic substance, or simply as *osteogen.* They exhibit faint fibrillation, and have been compared to bundles of white connective tissue fibres, with which, in some situations,

they appear to be continuous (Gegenbaur). But although similar in chemical composition, they are somewhat different from these in appearance, having a stiffer aspect and straighter course, besides being less distinctly fibrillated. The fibres become calcified by the deposition within them of earthy salts in the form of minute globules, which produce a darkish granular opacity, until the interstices between the globules also become calcified, and the minute globules becoming thus fused together, the new bone again looks comparatively clear (fig. 101, B, *b*).

As already stated the fibrils themselves are not calcified, but the calcification affects the portion of matrix which unites them into the osteogenic fibres, so that these may be described as being calcified.

The bundles of osteogenic fibres which prolong the bony spicules generally spread out from the end of each spicule so as to come in contact with those from adjacent spicules. When this happens, the innermost or proximal fibres frequently grow together (fig. 101, B, *c*), whilst the other fibres partially intercross as they grow further into the membrane. The ossific process extends into the osteogenic fibres *pari passu* with their growth, and thus new bony spicules become continually formed by calcification of the groups or bundles of osteogenic fibres.

The earthy deposit not only involves the osteogenic fibres, but also the ground-substance of the tissue in which they lie. It occasionally appears in an isolated patch here and there on some of the osteogenic fibres in advance of the main area of ossification (see fig. 101, A, *a*).

The osteogenic fibres become comparatively indistinct as they and the substance between them calcifies; they appear, however, to persist in the form of decussating fibres, such as are seen in the adult bone, although in the embryonic bone their disposition is less lamellated, the bony matter having a somewhat coarsely reticular structure.

In this way the first bony matter becomes formed as a perforated plate or network of osseous spicules, which, whilst becoming extended peripherally in the way above described, gradually becomes thicker nearer the centre, partly by the deposit of bony matter upon its surfaces, partly by the projection from them of bony spicules which are prolonged like those at the periphery by similar systems of osteogenic fibres. The perforations in these first-formed bony plates correspond to the bays which were seen between the advancing spicules, and to the meshes of the bony network formed afterwards by the junction of the spicules, and as the bone thickens they become enclosed and converted into reticulating interstices (like the canals of a sponge), which are occupied by blood-vessels, and by the corpuscles before mentioned. These corpuscles also everywhere cover the osteogenic fibres, to which their flattened sides are often applied (Fig. 101, B, *ost*). Where the osteogenic fibres diverge from one another, the intervals are occupied by the same cells. It is probable that the osteogenic substance is formed by the agency of the cells in question, hence the name "osteoblasts" was assigned to them by Gegenbaur. Some of the osteoblasts are involved in the ossifying matrix, and remain as the corpuscles of the future bone, the spaces enclosing them being the lacunæ. It is supposed that the canaliculi, which are at first short, are afterwards extended by absorption, so as to anastomose with those of neighbouring lacunæ.

It is believed by many histologists that the fibrillated ground-substance of bone is formed not outside the cells in an intercellular substance, but by a direct

conversion of the protoplasm of some of the osteoblasts into bony tissue. If this were the case, there ought to be some indication in the formed osseous substance of the cell-areas of which it was made up, but nothing of the kind has been shown to exist. There should moreover often be observed osteoblasts which are only partly converted into bony substance, but this has also never been described. And if as some suppose, the peripheral part of each osteoblast becomes converted into osseous substance, while the central part and nucleus remain as the corpuscle within a lacuna, the osteoblasts would have to be originally far larger than the permanent lacunæ, which is certainly not the case. The view in question is similar to that which supposes ordinary connective tissue to have a like origin, and appears to rest more upon theory than on actual observation of the stages of the developmental process.

Meanwhile, the meshes of the bony network, which were occupied as we have seen by one or more blood-vessels, and by numerous osteoblasts, become diminished in extent, and their walls, which were formed by the original trabeculæ, at the same time increased in thickness by the deposit upon them of irregular bony layers, some of the osteoblasts remaining between the layers, and forming the corpuscles and lacunæ as before. The interstices of the bony spongework thus become gradually converted into narrow channels in the osseous substance, containing one or more blood-vessels surrounded by osteoblasts.

At a later stage the increase in thickness takes place by successive depositions of bony lamellæ, under the periosteum, a concentric deposition occurring at the same time on the walls of the vascular channels. But since the growth in thickness of a membrane-bone takes place in exactly the same manner as that of one of the long bones, which will be fully described in a subsequent page, the reader is referred to the account of the process there given.

It may be observed that the appearance of the ossifying membrane-bone in the shape of a network of trabeculæ seems to be determined by the pre-existence of a vascular network in the embryonic tissue. The new bone everywhere makes its appearance in the spots which are furthest from the vessels, and the bony network everywhere alternates with the vascular network. At the edges of the advancing bone the spicules which prolong it pass between, and avoid the capillary blood-vessels, which are thus left in the bays between the spicules: the divergent bunches of osteogenic fibres which prolong the adjacent spicules complete the enclosure of the blood-vessel.

After a time the membrane-bone extends so as almost to come into contact with the neighbouring bones. But as long as growth continues, there always remains in the situation occupied afterwards by the sutures a vascular connective tissue with numerous osteoblasts. This is continually on the increase, but as fast as it grows, the osteogenic fibres and the osseous spicules extend into it from the young bones on either side. At length, however, when these have attained their full dimensions, the growth of the intermediate tissue ceases, and it becomes completely invaded by the bone on either side, with the exception of the narrow and irregular line of suture, which may eventually itself become more or less obliterated.

OSSIFICATION IN CARTILAGE.*

It has already been stated that, in by far the greater number of bones the mesodermic tissue with closely packed cells, of which they originally consist, is very quickly succeeded by cartilage, in which the ossification

* Different varieties of ossification in connection with cartilage are met with in the Vertebrata, and these are distinguished by comparative morphologists by special names. Thus when the calcareous deposit occurs immediately outside the perichondrium it is termed *parostosis;* immediately under the perichondrium, and eating into the cartilage, *ectostosis;* within the substance of the cartilage-matrix, *endostosis*, which again may be either superficial, or central (Parker & Bettany, Morphology of the Skull).

begins. One of the long bones taken from a very small embryo, just before ossification has commenced in it, is observed to be distinctly cartilaginous. In the tibia of a sheep, for example, at a time when the whole embryo is

Fig. 102.

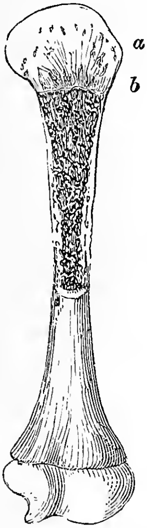

Fig. 102.—Humerus of a fœtus, natural size. (Sharpey.)

The upper half is divided longitudinally. *a*, cartilage, *b*, line of junction of bone and cartilage. The periosteal bone looks lighter than the endochondral bone proper.

Fig. 103.

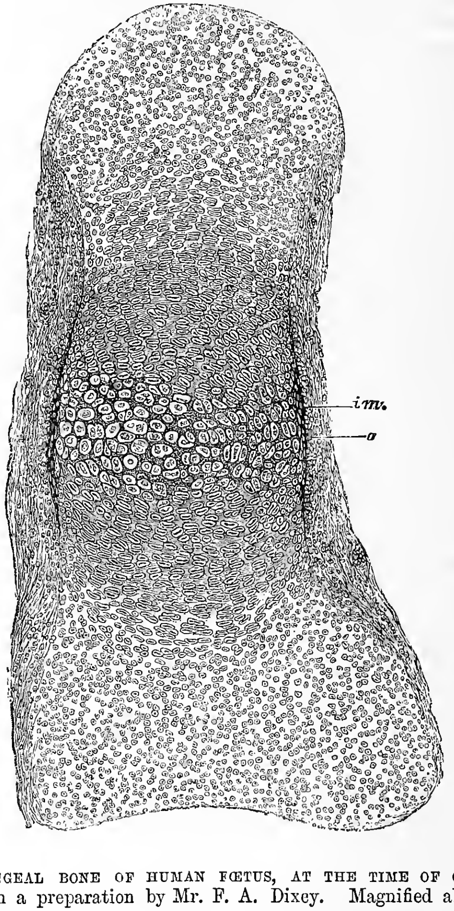

Fig. 103.—Section of phalangeal bone of human fœtus, at the time of commencing ossification. From a preparation by Mr. F. A. Dixey. Magnified about 75 diameters. (E.A.S.)

The cartilage cells in the centre are enlarged and separated from one another by dark-looking calcified matrix ; *im*, layer of bone deposited underneath the periosteum ; *o*, layer of osteoblasts by which this layer has been formed. Some of the osteoblasts are already embedded in the new bone as lacunæ. The cartilage-cells are becoming enlarged and flattened and arranged in rows above and below the calcified centre. At the ends of the cartilage the cells are small and the groups are irregularly arranged ; the fibrous periosteum is not sharply marked off from the cartilage.

not more than an inch and a quarter in length, we can plainly see that the substance consists of cartilage-cells imbedded in a pellucid matrix. These cells can scarcely be said to be collected into groups, and are very irregular in size and shape. They become enlarged in the middle

part of the shaft when ossification is about to commence. As it grows, the cartilage acquires firmer consistence; it represents in figure the future bone, though of course much smaller in size, and it is surrounded with a fibrous membrane, the future periosteum. Vessels ramify in this membrane, but none are seen in the cartilage until ossification is about to begin. In a long bone the ossification commences in the middle and proceeds towards the ends, which remain long cartilaginous, as represented in fig. 102. Much later, separate points of ossification appear in them, and form epiphyses, which at last are joined to the body of the bone.

The manner in which the process of ossification of a cartilage bone takes place is as follows:—

In the middle of the cartilage the cells are enlarged, and are separated from one another by a relatively larger amount of matrix than elsewhere (fig. 103). This matrix becomes hardened by calcareous deposit, assumes a granular opaque appearance, and has a gritty feel to the knife. Meanwhile the cartilage-cells above and below the centre of ossification become enlarged and flattened, and piled up in elongated groups or columns which radiate from the centre for a certain distance towards either end. The columns taper towards their ends, where the cartilage-cells which compose them are smaller. Into the matrix between these oblong groups the calcareous deposit extends between and around the groups of cells, so that the calcified substance encloses the columns; the cell-spaces in the calcified matrix which are still occupied by the cartilage-cells, either singly or in elongated groups, being termed the *primary areolæ* (Sharpey). Simultaneously with this deposit in the cartilage-matrix, a layer of osseous substance (fig. 103, *im*) is becoming formed on the outside of the cartilage underneath the periosteum. This last is a vascular membrane, containing numerous osteoblasts (*o*), which are chiefly collected on the inner surface next to the cartilage, and it is by their agency that the bony layer on the surface of the cartilage is formed and becomes increased both in thickness and length. The bony layer, when viewed on the surface, shows the usual component fibres of bony lamellæ, and as other layers are deposited upon it lacunæ become formed between them by the inclusion of some of the osteoblasts. In this first stage of ossification, we see therefore two processes going on, a deposit of earthy matter in the matrix of the cartilage, the cells of which assume a highly characteristic arrangement, and a deposition of true membrane-bone, underneath the perichondrium, and closely investing the surface of the cartilage.

What next happens is an irruption of the subperiosteal vascular and osteoblastic tissue into the middle of the cartilage, one or more apertures being excavated by absorption in the newly deposited osseous lamella and the tissue in question passing through these and burrowing into the cartilage (fig. 104, *ir*). Here it absorbs a great part of the calcified matrix, and by demolishing in this way parts of the walls of the primary areolæ, forms larger spaces (the *secondary areolæ* of Sharpey, the *medullary spaces* of H. Müller) which are filled by embryonic marrow, consisting of ramified cells and osteoblasts, the cartilage-cells which occupied the primary areolæ disappearing before it. All the middle of the calcified temporary cartilage becomes thus excavated with large spaces and replaced by the vascular osteoblastic tissue. As the calcification of the cartilage-matrix extends

towards the ends of the shaft, proceeding always in the same manner, the osteoblastic tissue closely follows, and after supplanting the cartilage-cells in the primary areolæ, absorbs parts of their walls so as to throw two or more together to form secondary areolæ ; in this way a great part of the primary bone (or calcified cartilage-matrix) is at once removed.

Fig. 104.

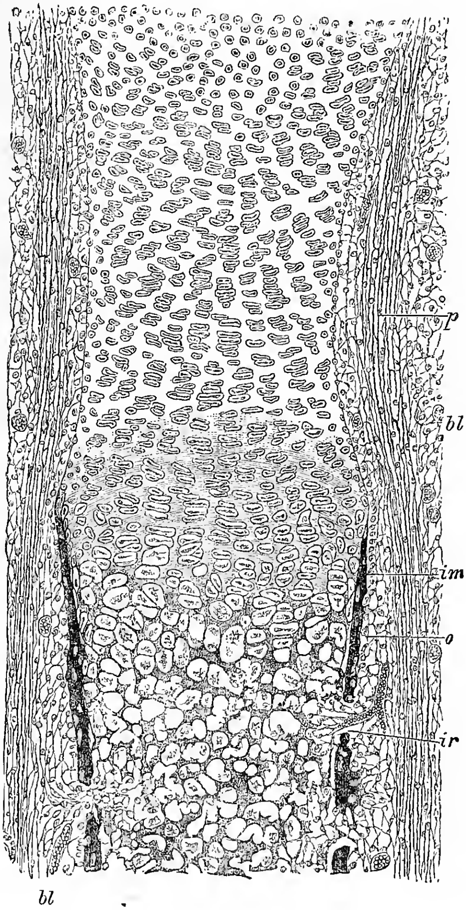

Fig. 104.—SECTION OF PART OF ONE OF THE LIMB BONES OF A FŒTAL CAT, AT A MORE ADVANCED STAGE OF OSSIFICATION THAN IS REPRESENTED IN FIG. 103, AND SOMEWHAT MORE HIGHLY MAGNIFIED. (Drawn by Mr. J. Lawrence.) (E.A.S.)

The calcification of the cartilage matrix has advanced from the centre, and is extending between the groups of cartilage cells which are now arranged in characteristic rows. The subperiosteal bony deposit (*im*) has extended *pari passu* with the calcification of the cartilage-matrix. The cartilage-cells in the primary areolæ are mostly shrunken and stellate, in some cases they have dropped out of the space. At *ir* and in two other places an irruption of the subperiosteal tissue, composed of ramified cells with osteoblasts and growing blood-vessels, has penetrated the subperiosteal bony crust, and has begun to excavate the secondary areolæ or medullary spaces ; *p*, fibrous layer of the periosteum ; *o*, layer of osteoblasts, some of them are embedded in the osseous layer as bone corpuscles in lacunæ ; *bl*, blood-vessels occupied by blood-corpuscles. B, beyond the line of ossific advance the periosteum may be noticed to be distinctly incurved. This incurvation is gradually moved on, the cartilage expanding behind it until the head of the bone is reached, when it forms the periosteal notch or groove represented in fig. 105, *p*.

At a short distance below the advancing ossification, the medullary spaces become at first somewhat more enlarged by further absorption, but at the same time their walls (which were at first formed only by the remains of the walls of the primary areolæ and therefore only by calcified cartilage-matrix) begin to be thickened by the deposition of layers of new bone, and this deposition increases gradually towards the middle of the shaft (compare fig. 108, *c* and *d*). The lacunæ first appear in this deposit, there are of course none in the

calcified cartilage. Moreover as layer after layer is deposited upon the walls of the medullary spaces these become gradually narrowed into

Fig. 105.

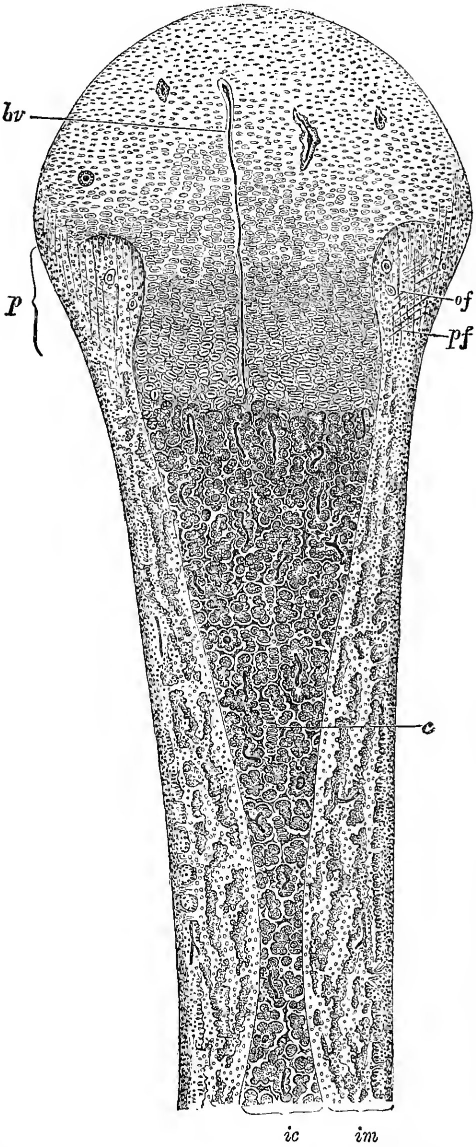

Fig. 105.—LONGITUDINAL SECTION THROUGH THE UPPER HALF OF THE DECALCIFIED HUMERUS OF A FŒTAL SHEEP, AS SEEN UNDER A MAGNIFYING POWER OF ABOUT 30 DIAMETERS. (Drawn by Mr. J. Lawrence.) (E.A.S.)

ic, the part of the shaft which was primarily ossified in cartilage; what remains of the primary bone is represented as dark, enveloped by the clear secondary deposit. The areolæ of the bone are occupied by embryonic marrow with osteoblasts, and blood-vessels variously cut, represented as dark lines. One long straight vessel (*bv* passes in advance of the line of ossification far into the cartilaginous head, most of the others loop round close to the cartilage. At one or two places in the older parts of the bone elongated groups of cartilage-cells (*c*) may still be seen which have escaped absorption. *im*, the part of the bone that has been ossified in membrane, that is to say in the osteoblastic tissue under the periosteum. It is well marked off from the central portion, and is bounded, peripherally, by a jagged edge, the projections of which are indistinctly seen to be prolonged by bunches of osteogenic fibres. A row of osteoblasts covers the superficial layer of the bone. The subperiosteal layer is prolonged above into the thickening (*p*), which encroaches upon the cartilage of the head of the bone, and in which are seen, amongst numerous osteoblasts and a few blood-vessels, the straight, longitudinal osteogenic fibres (*of*), and some other fibres (*pf*) crossing them, and perhaps representing fibres of Sharpey. The calcareous salts having been removed by an acid, the granular ossific deposit passing up between the rows of cartilage-cells is not seen in this specimen. Observe the general tendency of the osseous trabeculæ and the vascular channels between them to radiate from the original centre of ossification. This is found to prevail more or less in all bones when they are first formed, although the direction of the trabeculæ may afterwards become modified in relation with varying physiological conditions, and especially as the result of pressure in different directions.

inter-communicating channels, which contain little more than a blood-vessel and some jelly-like embryonic connective tissue (fœtal marrow) with a few osteoblasts applied to the bone.

In the end, some of the enlarged cavities and open structure remain to form the cancellated tissue, but much of this structure is afterwards removed by absorption, to give place to the medullary canal of the shaft. In many of these cavities the walls of the coalesced primary areolæ may long be distinguished, like little arches, forming by their union a sort of festooned outline, upon which the new bony laminæ are deposited (see figs. 105, & 109).

The *primary osseous matter* forming the original thin walls of the areolæ, and produced by calcification of the cartilaginous matrix, is decidedly granular, and has a dark appearance ; the subsequent or *secondary deposit* on the other hand is quite transparent, and of a uniform, homogeneous aspect. This secondary deposit begins to cover the granular bone a very short distance below the surface of ossification (see fig. 108), and, as already stated, increases in thickness further down.

Fig. 106.

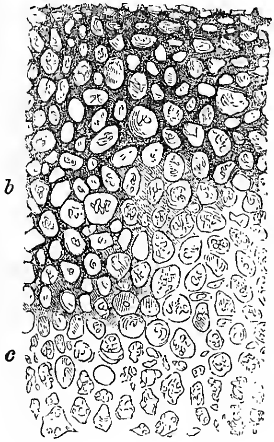

Fig. 107.

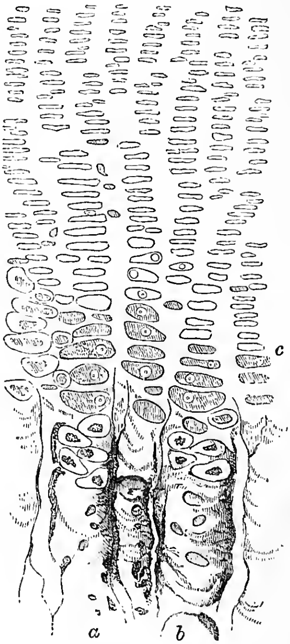

Fig. 106.—Transverse section of ossifying cartilage, including a portion of the advancing calcification. From the humerus of a fœtal sheep, magnified 70 diameters. (Sharpey.)

c, cartilage, the cells of which are enlarged, but the matrix not yet calcified ; *b*, primary osseous deposit in the cartilage matrix, extending between the cartilage-cells and enclosing them in primary areolæ.

Fig. 107.—Small portion of a section of developing bone, taken at the junction of the bone and cartilage, and examined in the fresh condition. Magnified about 140 diameters. (Sharpey.)

a, *b*, two of the new-formed osseous tubes or areolæ, with a few shrunken cartilage-cells lying in them ; *c*, cartilage-cells near the ossifying surface, large and clear and filling the cavities in the matrix ; on the left of the figure some of them are shrunken.

Close to the limit of advancing ossification, the blood-vessels terminate in capillary loops (see figs. 105, 108) which are often somewhat dilated. It is supposed by Ranvier that these vascular loops by their growth directly produce absorption of the cartilage, but it is more probable that this is caused by the agency of some of the cells which accompany the blood-vessels. The absorption of the walls of the primary areolæ (calcified cartilage-matrix) seems to be effected by certain large cells (fig. 108, *f,f*) which from their function have been termed by Kölliker, *osteoclasts*, and which are found wherever bone is being eaten away: we shall return to them further on. The secondary bone which thickens the walls of the medullary spaces is no doubt formed by the osteoblasts.

Fig. 108.

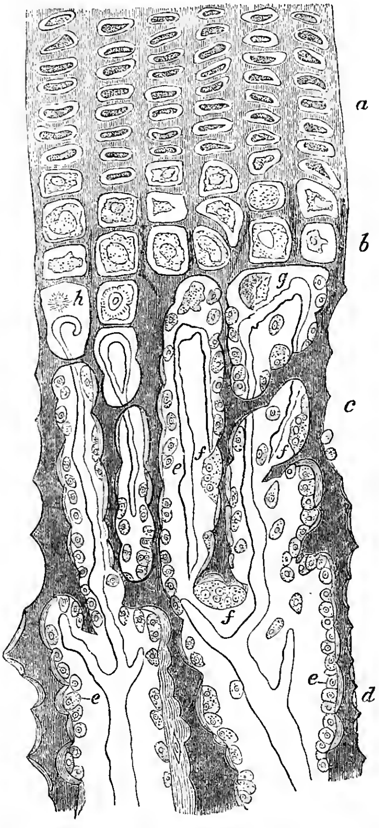

Fig. 108.—Part of a longitudinal section of the developing femur of the rabbit. Drawn under a magnifying power of 350 diameters (from Klein and Noble Smith).

a, rows of flattened cartilage-cells; *b*, greatly enlarged cartilage-cells close to the advancing bone, the matrix between is partly calcified; *c*, *d*, already formed bone, the osseous trabeculæ being covered with osteoblasts (*e*), except here and there, where a giant cell or osteoclast (*f*), is seen, eroding parts of the trabeculæ; *g*, *h*, cartilage-cells which have become shrunken and irregular in shape. From the middle of the figure downwards the dark trabeculæ, which are formed of calcified cartilage matrix, are becoming covered with secondary osseous substance deposited by the osteoblasts. The vascular loops at the extreme limit of the bone are well shown, as well as the abrupt disappearance of the cartilage-cells.

With regard to the destination of the cartilage-cells, two opposite views have been taken by histologists. According to one, which was that adopted by H. Müller, and has received most adherence, the capsules are opened by absorption, and the cells are converted, after undergoing division, into osteoblasts. According to the other, the cartilage-cells themselves become removed by absorption, and take no part, directly or indirectly, in the production of the secondary bone. The latter view of the matter was taken by Lovén, and it was also regarded by Sharpey as in all probability the more correct.

It is difficult to decide between these views. All that can be said is that the line of demarcation between the cartilage-cells and the osteoblastic tissue is exceedingly abrupt (fig. 108), and that the latter often, if not always, terminates either by a dilated vascular loop, or it may be by a developing capillary filled with blood corpuscles. Except that they are generally much shrunken and irregular in form (at least after death or the action of reagents), the cartilage-cells show no absorption and no distinct evidence of division, and it may be remarked that this is also the case when, as sometimes happens, they have not disappeared before the advancing subperiosteal tissue, but remain for a time still occupying an untouched primary areola (see fig. 105, *c*).

As ossification advances towards the ends of the bone, the portion as yet cartilaginous continues to grow at the same time, increasing in every dimension. The part already osseous increases also in circumference; fresh bone being continually deposited in the subperiosteal membranous tissue outside that which is first formed on the surface of the cartilage (figs. 105, 109). The subperiosteal deposit takes place in the same way as in the formation of a membrane bone. Bony spicules prolonged by bunches of osteogenic fibres (fig. 109, *o*) project out from the previously formed layer, into the intervals between the blood-vessels. By the union of the spicules these become in like manner enclosed in channels whose walls are gradually thickened by deposits of osseous lamellæ, between which some of the osteoblasts are left behind as bone-corpuscles in lacunæ, whilst others remain surrounding the blood-vessels in the vascular channels.

Fig. 109.

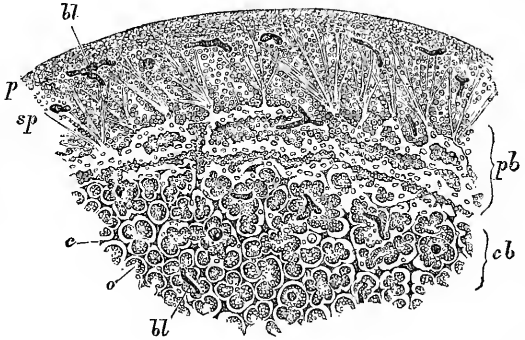

Fig. 109.—Part of a transverse section of a developing long bone, rather more advanced than that represented in fig. 105, and under a higher magnifying power (E.A.S.) From a drawing by Mr. J. Lawrence.

cb, endochondral bone which began as a calcification of the cartilage matrix, parts of which still remain (*c*) covered over by secondary osseous deposit; *o*, secondary areolæ, occupied by vessels, fœtal marrow, and osteoblasts; *pb*, periosteal bone deposited in the form of irregular trabeculæ, prolonged externally by bony spicules passing into bunches of osteogenic fibres. These, which are everywhere covered with osteoblasts, become lost in the external fibrous layer of the periosteum, *p*; *bl*, *bl*, blood-vessels variously cut.

The first formed bony tissue is different in its general appearance from the bony tissue of the adult, being more reticular and less regularly lamellar, and, for a long while, even the shafts of the long bones are rather cancellated, than compact in their texture. The more obviously lamellated condition does not begin to appear until about the sixth month after birth, when the periosteum deposits a succession of entire lamellæ around the embryonic bone. The blood-vessels which pass from the periosteum into the bone, pierce these circumferential lamellæ, but are not at first surrounded with concentric lamellæ, and do not therefore lie in true Haversian canals.* The latter become formed later by absorption taking place around the blood-vessels for some little dis-

* Even in the adult bone it may often be noticed that the blood-vessels which pierce the superficial lamellæ are not enclosed by Haversian systems.

tance, succeeded by a re-deposition of concentric lamellæ within the Haversian spaces thus formed.

Immediately before the occurrence of the lamellar deposition under the periosteum, the young bone undergoes a process of absorption from the inside. The medullary canal becomes thereby enlarged, and the medullary spaces, particularly those near the medullary canal, partaking of this absorption and enlargement, the result is that at about this period there is less bony matter in a section of the shaft than there was immediately before. To the change in question Schwalbe has given the name "osteoporosis;" it is followed by a re-deposition of osseous lamellæ both on the wall of the medullary canal, and on the walls of the medullary spaces of the embryonic osseous tissue.

Since the cartilage grows in every dimension by interstitial expansion, the bone which is invading it (endochondral bone) becomes gradually wider as the ossification advances. It is narrowest near the centre of the shaft where the process began, and widens gradually towards the ends; it has therefore somewhat of an hour-glass shape (fig. 105, *i.e.*). The cylindrical form of the shaft is maintained, however, by the thickness of the periosteal bone being greater at the

Fig. 110.

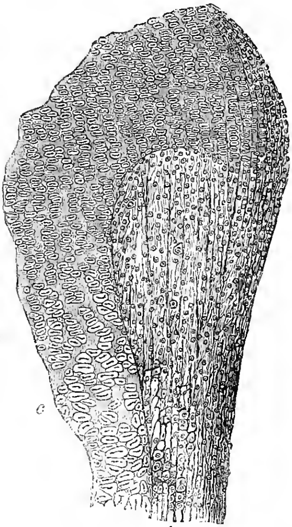

Fig. 110.—LONGITUDINAL SECTION THROUGH THE PERIOSTEAL THICKENING OF A BONE AT ABOUT THE SAME STAGE OF DEVELOPMENT AS THAT REPRESENTED IN FIG. 105. From a drawing by Mr. J. Lawrence. (E.A.S.)

c, cartilage with the cells in rows; the tissue of the periosteal thickening is sharply marked off from it except near the surface; *p*, outer layer of the periosteum; *i, p*, inner layer of the periosteum or subperiosteal tissue, with osteogenic fibres, and osteoblasts. One or two bloodvessels are observed cut across.

centre (where the deposition of bone first began, and has been longest proceeding) than at the ends. Here it gradually diminishes to a thin layer immediately investing that part of the cartilage into which the calcification is extending, so that the intramembranous subperiosteal ossification on the outside, may be said to closely accompany, if it does not even precede, the calcification of the cartilage in the interior. Either this investment of periosteal bone, or the calcification of the cartilage, seems to hinder the lateral expansion of that part of the cartilage in which the calcification is proceeding; but immediately beyond, the expansion already mentioned takes place. By the time that the ossification has advanced to the extremities of the shaft, the enlarged and expanded end of the cartilage has extended itself over the subperiosteal layer, so that this, with the accompanying osteoblastic tissue, now seems to lie in a groove or notch (fig. 105, *p*) in the cartilaginous head of the bone (Ranvier). This groove is filled with the same tissue as that which underlies the rest of the periosteum, namely a vascular tissue with branched cells and osteoblasts and osteogenic fibres. The latter are prolonged from the periosteal bone, and have for the most part a longitudinal direction (fig. 110).

Blood-vessels extend from the newly-formed osseous tissue beyond it into the cartilage. The vessels are lodged in excavations or branching canals in the cartilage (fig. 105) which also contain granular corpuscles (? osteoblasts). Other vascular canals enter the cartilage from its outer surface, and conduct vessels into it directly from the perichondrium.

The formation of osseous tissue, having thus proceeded for some time in the shaft, at length begins in the extremities of the bone from one or more independent centres, and extends through the cartilage, leaving, however, a thick

superficial layer of it unossified, which permanently covers the articular ends of the bone. The epiphyses thus formed are separated, as long as growth continues, from the shaft or diaphysis by an intervening portion of cartilage, which is at last ossified, and the bone is then consolidated.

A remarkable exception to the ordinary mode of ossification of the cartilage-bones occurs in the terminal phalanges of the digits. In these the calcification of the cartilage begins at the distal extremity or tip, and the sub-periosteal deposit appears simultaneously at the same point, and forms a cap-like expansion over the end of the phalanx. The irruption of the osteoblastic tissue also first occurs at this place. The expanded portion of the phalanx which bears the nail is formed independently of cartilage.

Growth and Absorption of Bone.—The time of final junction of the epiphyses is different in different bones; in many it does not arrive until the body has reached its full stature. Meanwhile, as above described, the bone increases in length by the ossification continuing to extend into the intervening cartilage, which goes on growing at the same time; and it appears that in the part of the shaft already ossified little or no elongation takes place by interstitial growth. This is shown by an experiment first made by Hales and afterwards by Duhamel and by John Hunter, in which, two or more holes being bored in the growing bone of a young animal at a certain measured distance from each other, they are found after a time not to be farther asunder, although the bone has in the mean while considerably increased in length. On the other hand, if one hole be bored in the epiphysis and another in the shaft, they become distinctly removed from one another with the growth of the bone. Moreover, it is well known that if the intervening cartilage in growing bone be injured by disease or removed by the knife, the growth of the bone in length permanently ceases.

Both Hales and Duhamel in experimenting on the growing tibia of a chicken, observed that the elongation was much greater at the upper end. Humphry has shown that in the arm bones the elongation is greater at the end furthest from the elbow joint, and in the leg bones at the end which is next the knee joint.

In the human subject between the first and the fourth or fifth years, the long bones grow chiefly in length, scarcely at all in thickness.

The shaft of a long bone increases in circumference by deposition of new bone on its external surface, while at the same time its medullary canal is enlarged by absorption from within. This can be determined by two methods of experimenting. Thus, in the first place, a ring of silver or platinum put round the wing bone of a growing pigeon, becomes covered with new bone from without, and the original bone included within it gets thinner, or, according to Duhamel, who first made the experiment, is entirely removed, so that the ring comes to lie within the enlarged medullary canal. Secondly, madder given to an animal along with its food tinges those parts in which deposition of new bone is taking place. The earth of bone appears to act as a sort of mordant, uniting with and fixing the colouring matter; and, as in this way the new osseous growth can be readily distinguished from the old, advantage was taken of the fact by Duhamel, and afterwards by Hunter, in their inquiries as to the manner in which bones increase in size. By their experiments it was shown that when madder is given to a young pig for some weeks, the external part of its bones is deeply reddened, proving that the new osseous matter is laid on at the surface of that previously formed. Again, it was found that, when the madder was discontinued for some time before the animal was killed, an exterior white stratum (the last formed) appeared above the red one, whilst the internal white part, which was situated within the red, and had been formed before any madder was given, had become much thinner; showing that absorption takes place from within. In this last modification of the experiment also, as noted by Hunter, a transverse red mark is observed near the ends of the bone, beyond which they are white; the red part indicating the growth in length during the use of the madder, and the white beyond, that which has taken place subsequently,—thus showing that the increase in length is caused by the addition of new matter to the extremities. Madder administered while the process of formation of the concentric lamellæ of the Haversian systems is going on, colours the interior and recently-formed laminæ, so that in a cross section the Haversian apertures appear surrounded with a red ring.

Flourens, and more recently, Kölliker, have repeated and varied these experiments, and have represented the results in beautiful delineations. Kölliker has, in addition, carefully investigated the microscopic appearances observed in the process of absorption of bone. From the results of his researches (which were in part anticipated by those of Lovén), it would seem that the process is essentially dependent on the presence of large multi-nucleated cells, by him termed "osteoclasts," identical with the "myeloplaxes" of Robin (see p. 100), which excavate, in the part which is undergoing absorption, small shallow pits (*foveolæ*) in which also they lie. These pits were first noticed by Howship: they seem to occur wherever absorption is proceeding, and it is to them that the festooned appearance of the Haversian spaces (p. 96) is due. The osteoclasts (fig. 111) vary in size, but are always many times larger than a blood-corpuscle: in shape they are spheroidal or flattened, with either an even or an irregular outline. Their substance is granular in appearance, and they each contain from two to ten clear round nuclei, but this number may be considerably exceeded, whilst on the other hand, there may be but one large nucleus provided with a number of bud-like projections. The osteoclasts frequently present on the side by which they are in contact with the bone a thickened striated border (fig. 111, *a*), somewhat similar to the well-known thickened base of the columnar epithelium-cells of the intestine. With respect to the origin and destiny of the osteoclasts, they are regarded by Kölliker both

Fig. 111.

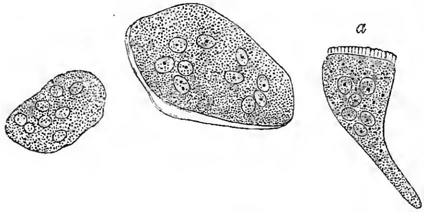

Fig. 111.—Three osteoclasts from absorption surfaces of growing bone. 400 diameters (Kölliker).

a, with thickened striated border.

as in the first instance derived from and as eventually breaking up into osteoblasts. Osteoclasts are found in connection with the roots of the milk teeth where these are undergoing absorption to make way for the permanent set; and cells precisely similar occur under pathological conditions in various situations quite apart from any hard tissue, and have long been known as "giant-cells" (Riesenzellen, Virchow.)

The changes of shape which the bones undergo in the process of growth, as well as any changes which may occur in them in adult life, are all produced in the same manner as the increase of size—that is to say, not by interstitial growth and expansion of the substance of the bone in one direction more than in another, but by a deposition of new bone by osteoblasts at some parts and a simultaneous absorption by osteoclasts at others; whilst in other places again neither absorption nor deposition is occurring—just as a modeller corrects his work by laying clay on at one part whilst removing it at another.*

Since during the growth of bones their shape is becoming continually altered, it follows that in nearly all bones during growth there are parts of the bone which are in process of absorption, and others which are in process of more active deposition than the rest. In most of the long bones, towards their ends, absorption is generally taking place at one side, and deposition on the opposite side. The former process may, and probably does, proceed to such an extent, that the endochondral bone may be laid bare or even partially absorbed, but after a while, when the absorption has ceased at any part, re-deposition may take place, the osteoclasts being replaced by osteoblasts, and successive circumferential lamellæ being deposited by these.

A large amount of variation is met with in the different bones of the skeleton

* For special details of this modelling process as it is met with in the different bones of the skeleton, the reader is referred to Kölliker's memoir; Die normale Resorption des Knochengewebes. Leipzig, 1873; and to a paper by Kassowitz (Die normale Ossification &c.) in Stricker's Med. Jahrb. 1879—1880.

in the relative extent to which they are formed in cartilage and in the sub-periosteal tissue respectively. Whereas in some, such as the long bones of the limbs, the endochondral bone is almost entirely removed, as we have seen, and periosteal bone substituted for it; in others, such as the bodies of the vertebræ, a much larger proportion of the adult bone has had an endochondral formation. In one or two bones or parts of bones again, which may be said to have typically an intramembranous origin, cartilage may, according to Kassowitz, become developed under the periosteum at certain places, and the continuation of the ossification may occur in this secondarily developed cartilage. This is said to be the case with the clavicle, the foundation of which is laid in membrane, but which is found at a later period to have cartilaginous ends; and also with the halves of the lower jaw-bone, which is said to develop cartilaginous ends both towards the symphysis and towards the articular and coronoid processes, these cartilaginous ends being altogether distinct from the cartilage of Meckel, which at those parts is unconnected with the jaw-bone, although at another place it is involved in the ossification of the maxilla (see vol. i., p. 74). Kassowitz has described also similar cartilaginous developments in connection with the sub-periosteal tissue at the tuberosity of the radius and the spine of the scapula.

The time of commencement of ossification in the different bones, as well as the number and mode of conjunction of their centres of ossification, have been treated of in the Descriptive Anatomy.

Regeneration of Bone.—In the reunion of fractured bones, osseous matter (which may be preceded by a new formation of cartilage), is formed between and around the broken ends, connecting them firmly together; and when a portion of bone dies, a growth of new bone very generally takes place to a greater or less extent, and the dead part is thrown off. The importance of the periosteum in the process of repair is shown by the fact that if a portion of periosteum be stripped off, the subjacent bone will be liable to die and exfoliate; conversely, if a large part or the whole of a bone be removed and the periosteum at the same time be left intact, the bone will, in a great measure, be regenerated. Osseous formation will even occur in connection with portions of periosteum which have been stripped away from the bone itself and intertwined amongst the muscles of the part, or even with portions that have been entirely removed from a bone and transplanted to a soft tissue. (Ollier.)

It is doubtful if the marrow-tissue can assist in the regeneration of bone. Experiments which have been made to determine this point would seem to show that although in the young bone, where the osteoblasts still retain their osteogenic function, the medullary tissue may take an active part in the formation of the first-formed new bone or "callus," in the adult no such participation of the marrow in the regeneration of bone takes place.

In the young subject even small pieces of the bone itself can be transplanted, and McEwen has succeeded in renewing the greater part of the excised humerus of a child by the introduction, at successive periods, of portions of fresh bone removed from another patient.

It was long supposed that all the bones of the skeleton were preceded by and deposited in cartilage. Nesbitt, however, showed in 1736 that some of the flat bones were formed independently of cartilage, and he further maintained that the cartilage is "entirely destroyed;" he therefore considered it to be a mere temporary substitute; but the steps of the process of intracartilaginous ossification as now traced with the aid of the microscope were unknown to him, and it was not until the year 1846 that the manner of formation of bone and the extensive replacement of the primarily ossified cartilage by new bone formed in membrane was made clear by the researches of Sharpey, who published the results of his work in the fifth edition of this book.

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MUSCULAR TISSUE.

The muscular tissue is that by means of which the active movements of the body are produced. It consists of fibres, which are for the most part collected into distinct organs called "muscles," and in this form it is familiarly known as the flesh of animals. These fibres are also disposed round the sides of cavities and between the coats of hollow viscera, forming strata of greater or less thickness. The muscular fibres are endowed with contractility, by virtue of which they shrink or contract more or less rapidly under the influence of certain causes which are capable of exciting or calling into play the property in question, and which are therefore named stimuli. A large class of muscles, comprehending those of locomotion, respiration, expression, and some others, are excited by the stimulus of the will, or volition, acting on them through the nerves; these are therefore named "voluntary muscles," although some of them habitually, and all occasionally, act also in obedience to other stimuli. There are other muscles or muscular fibres which are entirely withdrawn from the control of the will, such as those of the heart and intestinal canal, and these are accordingly named "involuntary." These two classes of muscles differ not only in the mode in which they are excited to act, but also to a certain extent in their anatomical characters; and on this account we shall consider the structure of each class separately.

STRUCTURE OF VOLUNTARY MUSCLES.

The voluntary muscular fibres are for the most part gathered into distinct masses or muscles of various sizes and shapes, but most generally of an oblong form, and furnished with tendons at each extremity, by which they are fixed to the bones.

The muscular fibres are collected into packets or bundles, of greater or less thickness, named *fasciculi* or *lacerti* (fig. 112). The fibres are parallel in the fasciculi; and the fasciculi extend continuously from one terminal tendon to the other, unless in those instances, like the rectus muscle of the abdomen and the digastric of the inferior maxilla, in which the fleshy part is interrupted by interposed tendinous tissue. The fasciculi also very generally run parallel, and, although in many instances they converge towards their tendinous attachment with various degrees of inclination, yet in the voluntary muscles they do not interlace with one another.

An outward investment or sheath of areolar tissue (*perimysium*) surrounds the entire muscle, and sends partitions inwards between the fasciculi; furnishing to each of them a special sheath. The areolar tissue extends also between the fibres (*endomysium*), but does not afford to each a continuous investment, and therefore cannot be said to form sheaths for them. Every fibre, it is true, has a tubular sheath; but this, as will be afterwards explained, is not composed of areolar tissue. The perimysium contains elastic as well as white fibres; but the elastic element is found principally in its investing (as distinguished from its penetrating) portion. In the endomysium numerous plasma-cells are found. The chief uses of the areolar tissue are to connect the fibres and fasciculi together, and to conduct and support the blood-vessels and nerves in their ramifications between the parts. The relation of these

different subdivisions of a muscle to each other, as well as the shape of the fasciculi and fibres, is well shown in transverse section (figs. 112 and 113).

Fig. 112.

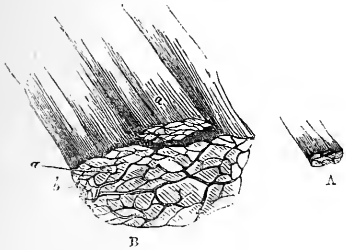

Fig. 113.

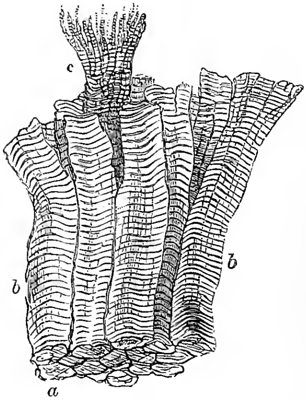

Fig. 112.—A, SMALL PORTION OF MUSCLE, CONSISTING OF LARGER AND SMALLER FASCICULI, NATURAL SIZE ; B, THE SAME MAGNIFIED 5 DIAMETERS, SHOWING A TRANSVERSE SECTION (Sharpey).

Fig. 113.—A FEW MUSCULAR FIBRES, BEING PART OF A SMALL FASCICULUS, MORE HIGHLY MAGNIFIED (Sharpey).

a, end view of *b*, *b*, fibres ; *c*, a fibre split into fibrils.

Fasciculi.—The fasciculi are of a prismatic figure, and their sections have therefore an angular outline (fig. 112). The number of fibres of which they consist varies, so that they differ in thickness, and a large fasciculus may be divisible into two or three orders of successively smaller bundles, but of no regularly diminishing magnitude. Some muscles have large, others only small fasciculi ; and the coarse or fine texture of a muscle, as recognized by the dissector, depends on this circumstance. The length of the fasciculi is not always proportioned to the length of the muscle, but depends on the arrangement of the tendons to which their extremities are attached. When the tendons are limited to the ends of a long muscle, as in the sartorius, the fasciculi, having to pass from one extremity to the other, are of great length ; but a long muscle may be made up of a series of short fasciculi attached obliquely to one or both sides of a tendon, which advances some way upon the surface or into the midst of the fleshy part, as in the instances of the rectus muscle of the thigh, and the tibialis posticus. Many short fasciculi connected thus to a long tendon, produce by their combined operation a more powerful effect than a few fasciculi running nearly the whole length of the muscle; but by the latter arrangement the extent of motion is greater, for the points of attachment are moved through a longer space.

Fibres ; their figure and measurement.—In shape the fibres are cylindrical, or prismatic with rounded angles. Their size is on the whole pretty uniform, although fibres occur here and there in a muscle which differ greatly in size from the prevailing standard. According to measurements by Kölliker in different regions of the body, the prevailing size of the fibres in the muscles of the trunk and limbs is

from $\frac{1}{750}$ to $\frac{1}{400}$ of an inch, but is less in those of the head, especially in the facial muscles, in which he found the diameter to range from $\frac{1}{750}$ down to $\frac{1}{2400}$ of an inch.

Fig. 114.

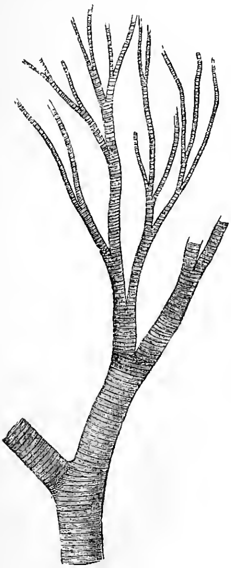

Fig. 114.—A BRANCHED MUSCULAR FIBRE FROM THE FROG'S TONGUE, MAGNIFIED 350 DIAM. (Kölliker.)

The fibres composing a muscle are of limited length, generally not exceeding one inch and a half; and accordingly in a long fasciculus a fibre does not reach from one tendinous attachment to the other, but ends with a rounded extremity, invested with its sarcolemma, and cohering with neighbouring fibres. Unless when either is fixed to a tendon, both extremities of the fibre terminate in the way described, so that it has a long cylindrical shape. In some muscles, e.g. the sartorius, fibres have been measured which are much longer than the dimension above given.

Generally speaking the fibres neither divide nor anastomose; but this rule is not without exception. In the tongue of the frog the muscular fibres (fig. 114) as they approach the surface divide into numerous branches, by which they are attached to the under surface of the mucous membrane. The same thing has also been seen in the tongue of man and various animals: and the fibres of the facial muscles of mammals divide in a similar manner where they fix themselves to the skin (Busk and Huxley).

Fig. 115.

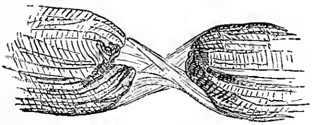

Fig. 115.—MUSCULAR FIBRE OF FISH. SUBSTANCE OF FIBRE RUPTURED SO AS TO EXHIBIT SARCOLEMMA. (After Bowman.)

Fig. 116.

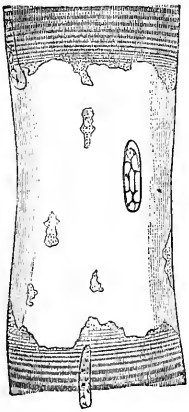

Fig. 116.—SARCOLEMMA OF MAMMALIAN MUSCLE, HIGHLY MAGNIFIED (E.A.S.).

The fibre is represented at a place where the muscular substance has become ruptured and has shrunk away, leaving the sarcolemma (with a nucleus adhering to it) clear. The fibre had been treated with serum acidulated with acetic acid.

Structure of the fibres; sarcolemma.—A muscular fibre may be said to consist of a soft contractile substance inclosed in a tubular sheath. The latter is named the *sarcolemma* or *myolemma*. It consists of transparent and apparently homogeneous membrane agreeing in physical and for the most part in chemical characters with elastic tissue, and, being comparatively tough, will sometimes remain entire when the included fibrils are ruptured by stretching the fibre, as represented in fig. 115. It is especially well seen in fish and amphibia, for in these it is thicker and stronger than in

mammalian muscle, in which it is more difficult to render evident but nevertheless always exists (fig. 116). Nuclei are found on the inner surface of the sarcolemma, but these belong rather to the contractile substance than to the inclosing membrane, and will be afterwards more fully described.

Contractile substance.—When viewed by transmitted light with a sufficiently high power of the microscope, the fibres, which are then clear and pellucid in aspect, appear marked with parallel stripes or bands alternately light and dark passing across them directly or somewhat obliquely with great regularity (fig. 117), and this not only at the surface but, as may be seen by altering the focus of the microscope, throughout its substance also. The dark and light bands are nearly of equal breadth, and when the fibre is much extended, a fine dark dotted line becomes visible in the middle of the light band, and dividing it into two. About eight or nine dark and as many light bands may be counted in the length of $\frac{1}{1000}$ of an inch, which would give about $\frac{1}{17000}$ inch as the breadth of each. But whilst this may be assigned as their usual breadth in human muscle, they are in different parts found to be much narrower, so that not unfrequently there are twice as many in the space mentioned. This closer approximation may generally be noticed in thicker and apparently contracted parts of the fibre. The cross-striped appearance, which is very characteristic, is found in all the voluntary muscles; but it is not altogether confined to them, for it is seen in the fibres of the heart, which is a strictly involuntary organ : striped fibres are also found in the pharynx and upper part of the gullet, in the muscles of the internal ear, and those of the urethra, parts which are not under the direct control of the will.

Fig. 117.

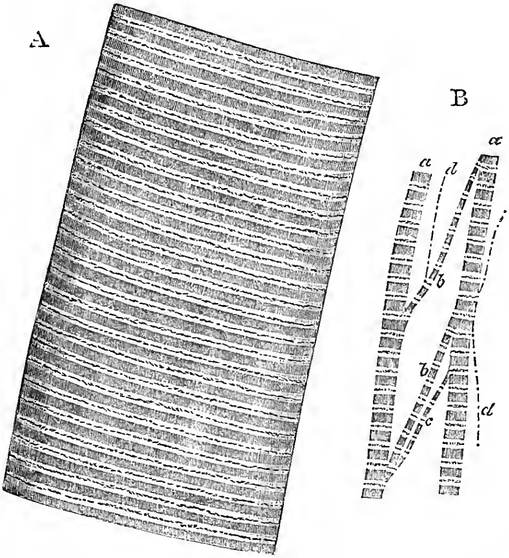

Fig. 117.—A, PORTION OF A MEDIUM-SIZED HUMAN MUSCULAR FIBRE, MAGNIFIED NEARLY 800 DIAMETERS (Sharpey).

B, SEPARATED PORTION OF A FIBRE, EQUALLY MAGNIFIED. *a*, *a*, larger, and *b*, *b*, smaller collections of fibrils ; *c*, still smaller ; *d*, *d*, the smallest which could be detached.

Fibrils ; disks ; sarcous elements.—The proper substance of the fibre presents, besides the transverse bands, an appearance of longitudinal striation, which is the better marked where the transverse striation is less distinct. On separating the fibre with needles, especially after hardening in alcohol, it may be broken up longitudinally into the so-

called *fibrils*, which, when of a certain fineness, appear to consist of a row of dark quadrangular particles (fig. 117, B, *b*), with bright intervals, the latter traversed by a dark dotted line, *c*, when the fibre is sufficiently extended. These rows of quadrangular particles which are sometimes taken to represent the sarcous elements of Bowman (see below) may, however, be further separated, as was shown by Sharpey, and the finest filaments so obtainable present the appearance of lines regularly broken at short distances (*d*). Each such thread may perhaps be looked upon as an ultimate fibril. It must, however, be borne in mind that the fibre is not wholly composed of these fibrils, but that there is in addition a not inconsiderable amount of intermediate substance.

Under other circumstances, as after the action of dilute acids or of gastric juice, the fibres show a tendency to cleave across in a direction parallel to the bands, and even to break up into transverse plates or disks, which are formed by the lateral cohesion of the particles of adjacent fibrils. To make up such a disk, therefore, every fibril contributes a particle, which separates from those of its own fibril, but coheres with its neighbours on each side, and this with perfect regularity. From a consideration of these facts, therefore, Bowman was led to conclude the subdivision of a fibre into fibrillæ to be merely a phenomenon of the same kind as the separation into disks, only of more common occurrence, the cleavage in the latter case taking place longitudinally instead of transversely: accordingly, he came to the conclusion that the fibrillæ have no existence as such in the fibre, any more than the disks ; but that both the one and the other owe their origin to the regular arrangement of the particles of the fibre (sarcous elements) longitudinally and transversely, whereby, on the application of a severing force, it cleaves in the one or in the other direction into regular segments.

Fig. 118.

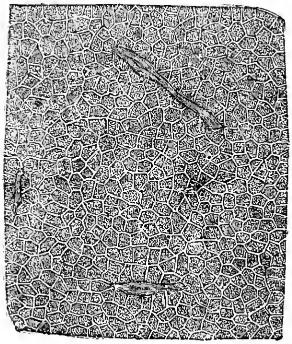

Fig. 118.—Transverse section of portion of muscular fibre of lobster. Examined in salt solution ($\frac{1}{2}$ per cent.) and magnified 400 diameters (Kölliker).

The polygonal areas of Cohnheim are seen, and among them two or three irregular nuclei.

If a transverse section of a muscular fibre is examined with a high power, it often appears to be marked out into small polygonal areas (Cohnheim) separated by clear lines (fig. 118). These areas are usually regarded as representing sections of the fibrillæ, but they would seem rather to correspond to groupings of the ultimate fibrillæ, for the fibrillæ are much smaller than the areas (compare fig. 117, B, *d*). Moreover, the areas may often be seen to have a punctated appearance, as if made up of the sections of a number of smaller elements. It must not be forgotten that the separation of a muscular fibre into disks or into fibrillæ is only possible after the coagulation of the muscle-plasma, or the action of re-agents upon it.

If perfectly fresh mammalian muscle is examined very carefully with

high powers, especially if the upper surface of the fibre is focussed, the striæ present the appearance shown in fig. 119, which on a smaller scale recalls that of insect muscle, as shown in fig. 120. By varying the focus this appearance and that exhibited in fig. 117 may often be obtained alternately, showing that optical conditions have much to do with the subjective effects produced by the examination of this tissue.

Muscle-nuclei or muscle-corpuscles.—In connexion with the cross-striated substance a number of clear oval nuclei are found in the fibres. In mammalian muscles they lie upon the inner surface of the sarcolemma (figs. 116, 119), but in frogs they are distributed through the substance of the fibre. Associated with and surrounding them there is sometimes, but not always, to be seen a certain amount of granular protoplasm, which shades off at the margins into the contractile substance of the fibre. Both substances are derived from the original formative protoplasm of the embryonic cells which compose the muscle (Max Schultze). In the unaltered condition the nuclei are not easily seen, but they may be made conspicuous by the addition of acetic acid. They contain a network of nucleoplasm, in which one or two nucleoli are generally visible.

Fig. 119.

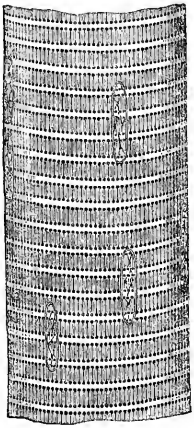

Fig. 119. —MUSCULAR FIBRE OF A MAMMAL EXAMINED FRESH IN SERUM, HIGHLY MAGNIFIED. (E. A. S.)

The nuclei are seen on the flat at the surface of the fibre, and in profile at the edges.

In the rabbit and hare, as especially pointed out by Ranvier, certain of the voluntary muscles present differences in appearance and mode of action from the rest. Thus while most of the voluntary muscles have a pale aspect and contract energetically when stimulated, some such as the semi-tendinosus and the soleus in the lower limb, are at once distinguished by their deeper colour as well as by their slow and prolonged contraction when stimulated. When subjected to microscopical examination it is found that in the red muscle the fibres are more distinctly striated longitudinally and the transverse striæ are much more irregular than usual. The nuclei also are far more numerous and are not confined to the inner surface of the sarcolemma, but occur here and there in the thickness of the fibre as well. There is also a difference in the blood-supply of the two kinds of muscle, to be afterwards alluded to.

A similar difference between red and pale muscles may be also seen in the Rays amongst fishes. In other animals the distinction is not found as regards whole muscles although it may affect individual fibres of a muscle. This is especially the case, according to Klein, in the diaphragm, in which in many of the fibres there are numerous nuclei, and these are embedded in protoplasm, which forms an almost continuous layer underneath the sarcolemma. The peculiarities in question seem to be dependent upon the amount of work which a muscle is habitually called upon to perform, and are probably connected with the nutrition and renovation of the muscle-substance (Meyer).

From the difficulty of making out all the details of structure of the mammalian muscle, arising from the extreme delicacy of its component elements and their liability to changes, histologists have availed themselves of the facilities afforded by the muscular fibres of insects, in which the elements are relatively large, and in which the fibres can be readily isolated in an unaltered and still contractile condition.

If a piece of one of the muscles which move the legs be removed from the

abdomen of one of the common water-beetles (Dytiscus marginalis), and whilst still fresh and living be examined, either in the blood of the insect or without the addition of any fluid, with a high power of the microscope. most of the fibres are seen to present, like mammalian muscle, the appearance of alternate dim and bright transverse bands. Each dim band is traversed by a series of fine lines set side by side, which refract the light more strongly than the rest of the muscular substance, and hence appear somewhat darker (fig. 120, *d*). Crossing the fibre in the middle of each of the bright stripes a double row of dots (*c*) is apparent; and on close inspection it may be seen that each line of the dim stripe is traceable at either end into one of the dots of the bright stripe; as if the dots were the enlarged ends of the lines. Thus the structure which the lines and dots indicate, belongs both to the dim and to the clear bands, the interval between the double row of dots corresponding to the middle of the clear band. In an optical transverse section of a fibre it may easily be seen that the lines in question represent rod-shaped structures, and not partitions in the fibre, as some have supposed, for they appear in cross-section as minute dots separated by clear interstitial

Fig. 120.

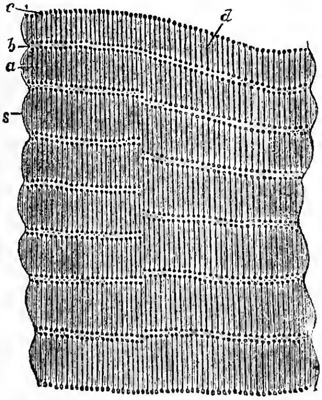

Fig. 120.—Living muscle of water-beetle (dytiscus marginalis). Highly magnified. (E. A. S.)

s, sarcolemma; *a*, dim stripe; *b*, bright stripe; *c*, row of dots in bright stripe, which seem to be the enlarged ends of rod-shaped particles, *d*.

Fig. 121.

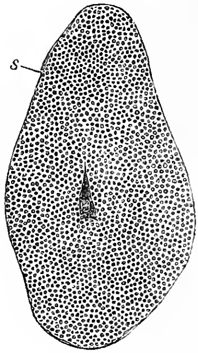

Fig. 121.—Transverse section of a muscular fibre of water-beetle. Highly magnified.

s, sarcolemma.

substance (fig. 121). The light and dark stripes are not sharply marked off from one another, nor is their line of junction an even one, for, on careful inspection, it is seen to be crenated, each crenation corresponding to a dot, the appearance being like that which would be produced if there were a clear halo around each of the dots, and as if the successive haloes had blended together to form the bright band.

Now it is familiar to microscopical observers that whenever any strongly refracting particle, such as a micrococcus or a minute oil globule, is examined in water with a high power of the microscope, it appears surrounded by a bright halo due to its refracting effect upon the light, and perhaps partly to the reflexion from its surface. And a row of micrococci seems to lie in a bright line due to the blending of the successive haloes formed around each one. If we assume, then, as the appearance of the transverse section would seem to justify us in doing, that the lines shown in fig. 120 are the expression of rod-like bodies with knobbed ends (muscle-rods), which ends correspond in situation with the bright striæ, such a view would completely account for the brightness of the latter. and has, moreover, the advantage that it offers a simple explanation of the appearance presented by the

living fibre. We should define the latter as consisting of two substances, not bright and dim, but of the substance of the rods and of interstitial substance, the bright appearance of the latter, in the situation of the light bands, being caused by the peculiar shape of the ends of the rods. The probability that this is the cause is increased by the fact that in some of the fibres the rods are cylindrical with their ends not enlarged and in contact, and in such cases the bright transverse bands are no longer observed. And it is further rendered probable by the appearances which can be observed in the living muscular fibre if it be closely watched during the passage of a contractile wave along its substance. These appearances may next be described.

Fig. 122.

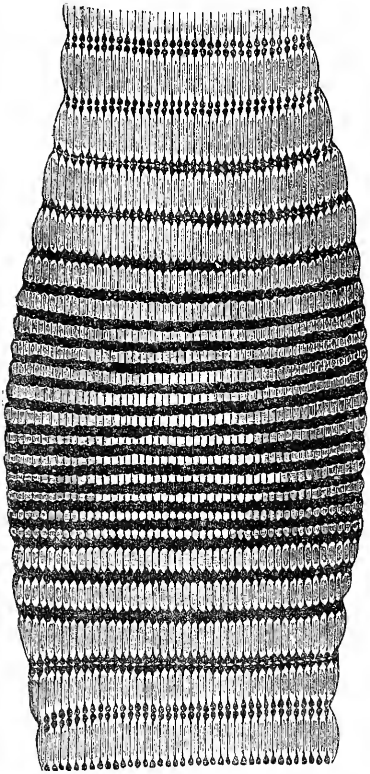

Fig. 122.—WAVE OF CONTRACTION PASSING OVER A MUSCULAR FIBRE OF DYTISCUS. VERY HIGHLY MAGNIFIED. (E. A. S.)

R, R, portions of the fibre at rest; C, contracted part.

CHANGES WHICH THE MUSCULAR ELEMENTS UNDERGO IN CONTRACTION.—When a portion of the still living muscular tissue of the water-beetle is observed under the microscope, contractions may be seen passing in waves along the fibres from end to end, and with care the following changes may be made out (fig. 122). That part of a fibre which is undergoing contraction becomes shorter and thicker. The two lines of dots in the middle of each bright band become blended to form a single dark line which is approximated to the neighbouring rows and gradually thickened, an appearance which suggests that the heads of the muscle-rods become enlarged at the expense of the connecting stems. Dark bands are thus formed occupying the situation of the previous bright bands with their double rows of dots, whilst the dim bands which alternated with these are much reduced in thickness, and partly by contrast, partly in all probability by reflexion from the surface of the newly formed bands, are relatively clear and brilliant. For in consequence of the enlargements of the dots and their blending into a continuous disk, the bright effect which they produce instead of appearing as a series of haloes as in the resting muscle, extends to the whole of the now diminished interval between the successive series, and this moreover tends to render obscure the attenuated shafts.

It will be seen that in the process of contraction the relative position of the light and dark parts of the fibre has become altered, so that the band which was previously dim is now bright.*

The muscles which move the wings of insects present certain points of difference from those of the legs which have just been described. They are readily

* For a further account of this subject the reader is referred to a paper on the Leg-Muscles of the Water-Beetle, in the Phil. Trans. 1873.

dissociated, even in the fresh condition, into very small fibres or fibrils which are collected into bundles surrounded by the ramifications of the air-tubes or tracheæ. Each separated fibre, if sufficiently extended (fig. 123, C), is composed of alternate dark and light disks, and in the middle of the light disk there is seen a fine sharply marked intermediate dark line *m*, but the appearances vary much according to the state of extension of the fibril (see fig. 123). No rod-like structure had, until quite recently, been detected in these fibrils of the wing-muscles, and this was believed to constitute an essential distinction between them and the ordinary muscles, but with the aid of improved objectives Wagener has been able to detect fine longitudinal elements in the former also.

Fig. 123.

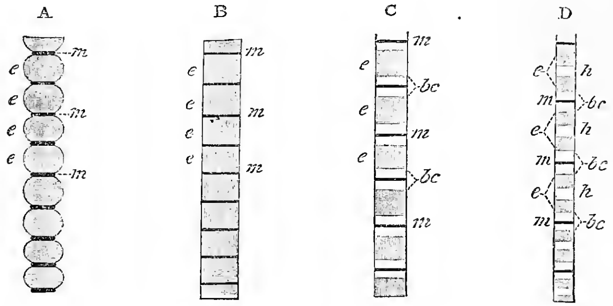

Fig. 123.—Fibres of the wing-muscles of an insect (after Ranvier).

The fibres are in different conditions of extension, from A least extended, to D most extended. *e*, *e*, chief substance of the fibre; *m*, *m*, intermediate lines or disks; the light bands, *bc*, on either side of these only come to view when the fibre is sufficiently stretched (C); with further extension (D), the middle of the dark band appears lighter, *h*.

Brücke's observations upon the appearances of muscle under polarized light.—It was noticed by Boeck that, like some of the other tissues, muscle is doubly refracting (anisotropous). Brücke however was the first to point out that the fibre is not composed entirely of anisotropous substance, but that there is in addition a certain amount of singly refracting or isotropous material. Since the important researches of the last-named author form the basis of our knowledge of this subject, a short account will be given of them here.

In the first place Brücke distinguishes between the appearances presented by living muscle examined in its own plasma and those of dead and prepared muscle. In dead muscle, although a considerable variation is noticeable in the relative amount of anisotropous and isotropous substance, nevertheless the two substances invariably take the form of alternating bands, dark and light, crossing the fibre and apparently corresponding in position with the light and dark stripes of the fibre as seen under ordinary light.

It is quite otherwise with living muscle. In this almost the whole of the fibre looks doubly refractile, the isotropous substance occurring only as fine transverse lines, or as rows of rhomboid dots which are united to one another across the anisotropous substance by fine longitudinal lines. This account is illustrated by fig. 124, which is copied from Brücke. Now if this figure be compared with fig. 120, or with the parts marked R of fig. 122, which represent the living muscle of a water-beetle under ordinary light, it is obvious that the rhomboid points and longitudinal lines of the one correspond to the muscle-rods of the other. The substance of the rods there-

fore, is singly refracting, whereas the substance between them is doubly refracting.*

Brücke has applied the theory of Bartholin, invented to explain the phenomena of double refraction in crystals of Iceland spar, and which supposes that those crystals are compounded of minute doubly refracting particles (disdiaclasts), to the doubly refracting substance of muscle, and has applied the same name (*disdiaclasts*) to the particles of which he supposes that substance to be composed, and which would appear to act upon the light like positive, uniaxial, doubly refracting crystals. Under certain circumstances, as after the action of water or salt solution the muscular substance is apt to break down into a cloud of fine doubly refracting particles which are either themselves the disdiaclasts or represent groups of them.

Fig. 124.

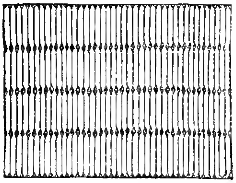

Fig. 125.—Living muscle of a water-beetle examined in polarized light with crossed Nichol's prisms (Brücke).

Other views of muscular structure.—Until Bowman published, in the Philosophical Transactions for 1840, his important work on the structure of muscle, the whole subject was exceedingly obscure. The view which Bowman took of the constitution of muscular substance, namely, that it is composed of a series of particles joined together closely side by side into disks, and less intimately united end to end into fibrils, long occupied a dominant position in this branch of histology. Kölliker however (1851), laying stress upon the fact that the muscular substance is much more apt to break up into fibrils than into disks, looked upon the appearance of the latter as altogether secondary, and regarded the fibrils as the actual elements of the muscle, the alternate dark and light portions in the course of each fibril being of essentially the same nature, although differing somewhat in their optical properties. Afterwards (1867), recognising that the so-called fibrils were in reality made up of finer elements, the ultimate fibrils, Kölliker was led to term the structures formerly known as fibrils "muscle-columns," and he looked upon the areas of Cohnheim as representing the transverse sections of those columns.

W. Krause (1868) introduced an entirely new idea into the conception of the subject, by looking upon the intermediate line in the light stripe as a continuous disk or membrane, united laterally to the sarcolemma, and thus dividing the whole fibre into a series of flat compartments, these being again subdivided longitudinally by partitions (seen on transverse section as the clear lines bounding Cohnheim's areas), so that little cases (Muskel-kästchen) are thus formed (fig. 125, A). Each such case contains, according to Krause, a portion of the dark disk (muscle-prism) in its middle part, and portions of the light disks (fluid) at either end, and Krause supposed that in contraction this fluid changes its situation, becoming shifted to the periphery of the dark substance, and that in this way the muscle is diminished in length, and proportionally increased in breadth (fig. 125. B). Subsequently, however, recognising the existence of "muscle-rods" within the muscle-prism, Krause described the fluid as passing between the rods and separating them more from one another during contraction (C).

* In point of fact Brücke regarded the lines which traverse the anisotropous disks not as rod-like structures, but as the optical sections of partitions separating columnar portions of anisotropous substance from one another. But with a good lens it can be readily seen that the lines in question are not partitions but are isolated from one another, and this is still more obvious in the transverse section of the muscle (fig. 121). Taking into consideration this difference of terminology, my own observations upon the appearance of living muscle in polarized light agree entirely with those of Brücke. So far as I have been able to see, the muscle-rods are isotropous or singly refracting, the rest of the muscle-substance is anisotropous or doubly refracting. In contracted muscle the darker disks, which as before described are formed by the enlargement and apparent fusion of the knobbed ends of the rods, are singly refracting, the alternating light bands being doubly refracting. In dead muscle alternating singly and doubly refracting disks are almost always seen, even although the fibre may not appear to be contracted.

The next prominent writer upon the subject was Merkel (1872), who described the transverse membranes of Krause as being double, and who corroborated Hensen's description of the existence of a lighter line or disk in the middle of the dark stria. But the most important difference in Merkel's account occurs in his description of the process of contraction. According to him, the anisotropous substance of the dark stria first of all becomes diffused over the whole muscle-compartment, so that the fibre acquires a homogeneous appearance, and then at a later stage becomes accumulated against the transverse membranes, while the isotropous substance on the other hand is accumulated on either side of Hensen's disk, so that the position of the two substances is thus reversed.

Fig. 125.

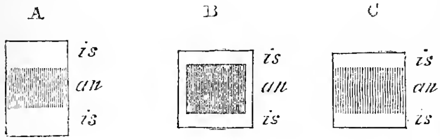

Fig. 125.—Diagrammatic representation of a muscle-case under a very high magnifying power (W. Krause).

A, at rest; B, condition in contraction, former view; C, condition in contraction, present view. *an*, muscle-prism, consisting of a bundle of muscle-rods; *is*, fluid isotropous substance.

Merkel was closely followed by Engelmann (1873), according to whose description, a muscular fibre consists of a succession of superimposed parts or compartments, which are partitioned off from one another by thin disks or membranes—Krause's membranes or intermediate disks (fig. 126, *a a*)—which may occasionally be double. Within each compartment is a series of disks, varying in their refractive power and in their action upon polarized light, as follows:—Next to an intermediate disk comes a comparatively narrow layer of isotropous clear substance, then a thin disk of dim substance, which is feebly anisotropous, and is distinguished as the accessory disk, (*b*); this is followed by a narrow layer of clear isotropous substance; then comes a broad disk of anisotropous substance (principal disk, *c*), occupying the greater portion of the muscle-compartment, and sometimes bisected by a narrow pale disk, which lies exactly in the middle of the compartment, and is distinguished as the middle disk or disk of Hensen (not seen in the figure). Beyond the broad anisotropous disk come in inverse succession isotropous substance, accessory disk, and intermediate disk, and so on in the next compartment.

When contraction is about to supervene in any part of a muscular fibre, the changes, which according to Engelmann may be observed, are the following:—While the intermediate disks approach one another, the successive disks within each muscle-compartment become less distinct, and the fibre loses in great measure at the part in question (that namely in which the contraction is beginning), its striated appearance. The stage in question is accordingly termed by Engelmann the homogeneous stage (fig. 126, H.). As the contraction progresses, transverse striæ again make their appearance, in consequence of the gradual darkening of the accessory disks and concomitant clearing up of the principal disk, so that now each intermediate disk with its juxtaposed accessory disks forms a distinct dark isotropous band, these alternating with the narrowed and now bright-looking principal disks of anisotropous substance (fig. 126, C.) The reversal of the striæ in contracting muscle is ascribed by Engelmann wholly to changes in refrangibility in the several substances which compose the disks of the muscle-compartment accompanied by an increase in the volume of the principal disk at the expense of the isotropous substance.

With regard to the above account of the changes which occur during contraction, it should be mentioned that it is not founded upon the observation of the contractile change as it may be seen to occur in the living muscle, but on the examination of the so-called "fixed waves of contraction," which are seen in fibres of muscles obtained from insects which have been killed by being placed in osmic acid or alcohol. On such fibres it often happens that

one or more swellings occur upon the otherwise extended fibre, and these swellings are assumed to be contractile waves, which have been fixed during their passage along the fibre by the sudden influx of the reagent, it being taken for granted that the reagents in question fix the living muscular fibres in exactly the same condition as at the time of immersion. But this assumption is not borne out by the facts of the case. For if the living muscular tissue of an insect is being observed under the microscope, and a drop of osmic acid or of alcohol is allowed to come into contact with it, the whole fibre if free to contract at once does so, and remains contracted. Moreover, as the reagent penetrates the substance of a fibre, the appearance of the latter becomes profoundly modified in place of remaining unaltered as asserted by Engelmann. If the ends of the muscle are fixed so that it is not free to contract, the general shortening of the

Fig. 126.

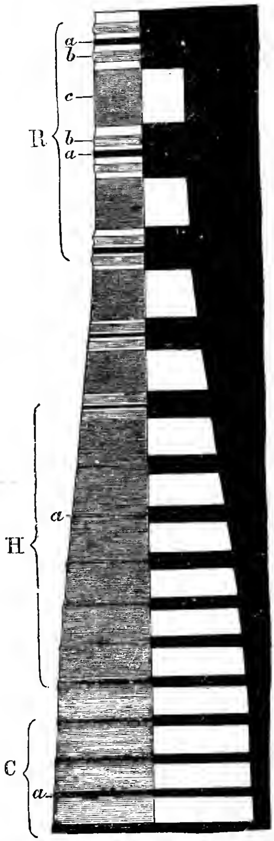

Fig. 126.—Muscular fibre of an insect, exhibiting a part of one of the so-called "fixed waves of contraction" (from Engelmann).

The right half of the figure shows the effect produced by the same fibre when examined under polarized light, the principal disks then appearing light on the dark field caused by the crossed Nichols' prisms.

R, part at rest, or at least extended; H, homogeneous part; C, contracted part. *a*, intermediate disk; *b*, accessory disk; *c*, principal disk.

fibre and the approximation of the discs may not occur except here and there, and at these places the swellings known as fixed waves of contraction manifest themselves, but it by no means follows that in the intermediate parts the fibre, although extended, is not, so far as regards the arrangement of its elements, in the condition that ordinarily accompanies contraction. The homogeneous appearance at the rise and fall of the "fixed wave," may be accounted for if we consider that the longitudinal elements are liable to become shifted somewhat by the shortening of a neighbouring part of the fibre, for it is well known that mechanical shifting of the elements of a fibre causes a disappearance of the transverse striation.

Ranvier (1880) reverts to a view of muscle-structure which is similar to that of Krause, but gives an entirely different account of the changes which accompany contraction.

Whatever may be the interpretation put upon the appearances exhibited by muscle, there is little doubt that the contractile phenomena are of essentially the same nature in voluntary muscle as in involuntary muscle, and even as in cilia, and in the movements of simple protoplasmic cells. Both the contraction of muscle and the contraction of protoplasm are dependent upon the maintenance of nutrition, and are influenced similarly by external conditions. The only striking point of difference, apart from the relative quickness or slowness with which stimuli are responded to, lies in the fact that in muscle, whether voluntary or involuntary, the contraction is confined to one dimension, whereas ordinary protoplasm is capable of contracting in any direction. That in the living condition the substance of a muscular fibre is, like protoplasm, of a semi-fluid nature, was proved by the

oft-quoted observation of Kühne (repeated by Eberth), who observed a minute parasitic worm moving in the interior of a living muscular fibre of the frog, and noticed that the transverse striæ and other markings in the fibre which were displaced by the movements of the worm, closed in again behind it, reassuming their proper order and former position.

Mode of Attachment of Muscular Fibres: Ending of Muscle in Tendon.—When a muscle ends in a tendon it is found that the muscular fibres either run in the same direction as the tendon-bundles or join with the tendon at an acute angle. In the former case the tendon becomes subdivided, either gradually or suddenly, into as many small bundles as there are fibres in the end of the muscle, and it often seems at first sight as if the tendon-fibres were directly continued into the muscular substance. In reality, however, the fibres of each tendon-bundle end abruptly on reaching the rounded or obliquely truncated extremity of a muscular fibre (fig. 127), and are so intimately united to the prolongation of sarcolemma which covers the extremity, as to render the separation between the two difficult if not impossible (Ranvier). The muscular substance, on the other hand, may readily be caused to retract from the sarcolemma at this point. The areolar tissue which lies between the tendon-bundles, passes between the ends of the muscular fibres and is gradually lost in the interstitial connective tissue of the muscle.

Fig. 127.

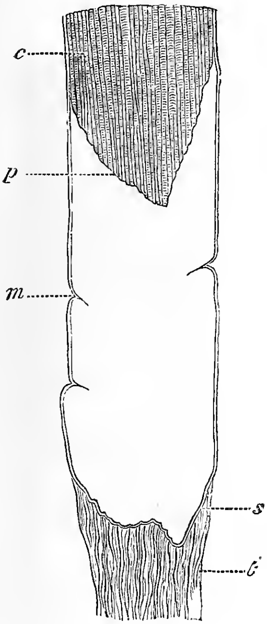

Fig. 127.—Termination of a muscular fibre in tendon (Ranvier).

m, sarcolemma; *s*, the same membrane passing over the end of the fibre; *p*, extremity of muscular substance, *c*, retracted from the lower end of the sarcolemma-tube; *t*, tendon-bundle passing to be fixed to the sarcolemma.

When the direction of the muscular fibres is oblique to that of the tendon, the connection takes place in a similar way to that above described, but the small tendon bundles are given off laterally along the course of the tendon, which in these cases is generally prolonged into or over the muscle.

When the muscular fibres divide, each branch of the fibre is described as being directly continuous with a tendon-bundle, or connective tissue bundle, without the intervention of sarcolemma, but it is not improbable that renewed careful investigation might, in this case also, disclose the existence of a thin prolongation of sarcolemma over the divisions.

Blood-vessels.—The blood-vessels of the muscular tissue are very abundant, so that, when they are successfully filled with coloured injection, the fleshy part of the muscle contrasts strongly with its tendons. The arteries, accompanied by their associate veins, enter the muscle at various points, and divide into branches: these pass among the fasciculi, crossing over them, and dividing more and more as they get

between the finer divisions of the muscle; at length, penetrating the smallest fasciculi, they end in capillary vessels, which run between the fibres. The vessels are supported in their progress by the subdivisions of the sheath of the muscle, to which also they supply capillaries. The capillaries destined for the proper tissue of the muscle are extremely small; they form among the fibres a fine net-work, with narrow oblong meshes (fig. 128), which are stretched out in the direction of the fibres; in other words, they consist of longitudinal and transverse vessels, the former running parallel with the muscular fibres, and lying in the angular intervals between them,—the latter, which are much shorter, crossing between the longitudinal ones, and passing over or under the intervening fibres.

Fig. 128.

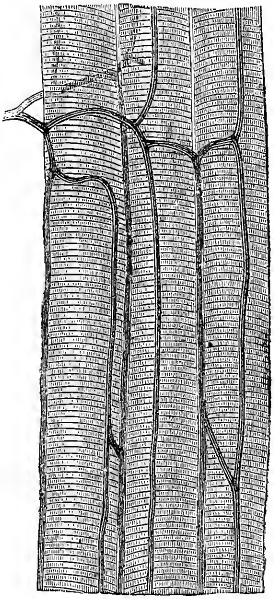

Fig. 128.—Capillary vessels of muscle, moderately magnified. (E.A.S.)

In the deeper coloured muscular fibres of those animals which, like the rabbit, possess two kinds of voluntary muscles, the transverse loops of the capillary net-work are dilated far beyond the size of the ordinary capillaries.

The number of capillaries in a given space of a muscle, or their degree of closeness is partly regulated by the size of the fibres; and accordingly in the muscles of different animals it is found that, when the fibres are small, the vessels are numerous and form a close network, and *vice versâ:* in other words, the smaller the fibres, the greater is the quantity of blood supplied to the same bulk of muscle. In conformity with this, we see that in birds and mammalia, in which the process of nutrition is active, and where the rapid change requires a copious supply of material, the muscular fibres are much smaller and the vessels more numerous than in cold-blooded animals, in which the opposite conditions prevail.

Lymphatics.—So far as is known there are no lymphatic vessels in the voluntary muscles, although there is an abundant supply in their connective tissue sheaths and tendons, and the lymphatic vessels here would seem, as pointed out by Ludwig and Schweigger-Seidel, to serve the purpose of collecting and conveying away the lymph from the muscular substance. How the fluid reaches the lymphatic vessels of the sheath is not certainly known: it may be by the medium of the intercommunicating spaces of the connective tissue which penetrates between the fasciculi and fibres of the muscle.

Nerves.—The nerves of a voluntary muscle are of considerable size. Their branches pass between the fasciculi, and repeatedly unite with each other in form of a plexus, which is for the most part confined to a small part of the length of the muscle, or muscular division in which it lies. From one or more of such primary plexuses, nervous twigs proceed, and form finer plexuses composed of slender bundles, each containing not more than two or three dark-bordered nerve-fibres, whence single fibres pass off between the muscular fibres and divide into

branches which are finally distributed to the tissue. The mode of final distribution will be described with the general anatomy of the nerves.

Nerves of small size accompany the branches of blood-vessels within muscles ; though destined for the vessels, these nerves are said sometimes to communicate with the proper muscular plexuses.

DEVELOPMENT OF VOLUNTARY MUSCULAR TISSUE.

Most of the voluntary muscles of the body are developed from a series of portions of mesoderm which are early set aside for this purpose in the embryo and are termed the muscle-plates. The cells which compose these are similar in most respects to those in the remainder of the mesoderm, but when the muscular fibres are about to be formed the cells become elongated, and their nuclei multiplied so that each cell is converted into a long multi-nucleated protoplasmic fibre. At first the substance of the fibre is not striated but is merely granular in appearance, but presently it becomes longitudinally striated along one side (fig. 129, A), and about the same time a delicate membrane, the sarcolemma, may be discovered bounding the fibre. The longitudinal striation, which is the first indication of the proper muscular substance, extends along the whole length of the fibre, but at first as just intimated affects only a small part of its breadth, the rest being formed by a highly glycogenic protoplasm containing the nuclei. In due time, however, this conversion into the proper muscular substance, further shown by the appearance of cross striæ (fig. 129, B and C), proceeds through the whole thickness of the fibre, and the nuclei take up their permanent position underneath the sarcolemma.

Fig. 129.

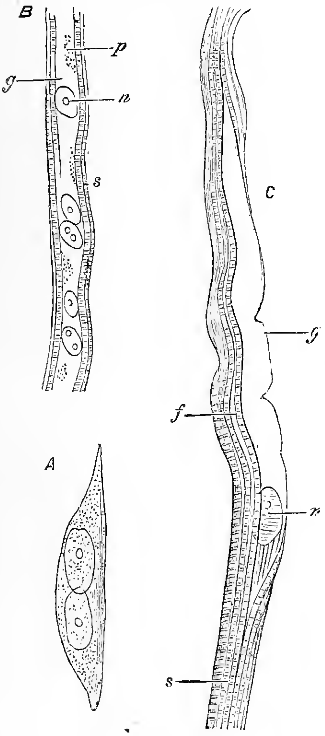

Fig. 129. — DEVELOPING MUSCULAR FIBRES. HIGHLY MAGNIFIED.

A, elongated cell with two nuclei and a striation beginning down one side of the cell (from fœtal sheep, Wilson Fox).

B, from fœtus of 2 months ; *p*, granular protoplasm ; *g*, glycogenous substance ; *n*, nucleus ; *s*, commencing sarcolemma, with striated muscular substance developing immediately beneath it.

C, from fœtus of 3 months, displayed so as to show the contractile substance collected at one side of the fibre, and partially enclosing the unaltered substance of the fibre, *g* ; *f*, fibrils. B and C from Ranvier.

Schwann considered each fibre to be formed by the linear coalescence of several cells ; but the researches of Kölliker, Wilson Fox, and others, tend to establish the view, originally promulgated by Remak, that the fibres are produced as above described by the elongation of single cells, with differentiation of their contents and multiplication of their nuclei.

Growth.—The muscular fibres, after having acquired their characteristic form and structure, continue to increase in size till the time of birth, and thenceforward up to adult age. In a full-grown fœtus most of them measure twice, and some of them three or four times their size at the middle of fœtal life ; and in the adult they are about five times as large as at birth. This increase in bulk of the individual fibres would, of course, so far account for the concomitant enlarge-

ment of the entire muscles. It is uncertain how far there may be a multiplication or new formation of muscular fibres during the growth of a muscle.

Regeneration.—It is generally stated that after removal by the knife or by disease striated muscular tissue is not regenerated, but that any breach of continuity which may occur in a muscle is filled up by a growth of connective tissue. It would appear, however, that the breach is eventually bridged across by muscular substance, the new muscular tissue in all probability being formed by the growth of the old muscular fibres into the connective tissue which unites the cut ends.

Nothing is certainly known about the actual process of waste and renewal which must be continually occurring in so active a tissue as the one in question. It is probable that in most cases the changes are molecular, and that the muscular fibres are never removed *in toto* by absorption. But the case may be otherwise in some animals, as, for example, in frogs, which in the winter season have many of their fibres destroyed by fatty degeneration. According to Beale and von Wittich these are replaced by the development of new fibres from cells which lie between the existing fibres, by a process analogous to the original development, but Weissmann and Kölliker state that the formation of new fibres may take place by the splitting up of the old fibres along their whole length.

INVOLUNTARY MUSCLES.

The involuntary muscular tissue differs from the voluntary kind, not only in some of its physiological properties but also in its anatomical characters ; for whilst in many parts it appears in the form of fibres, these, except in the heart and a few instances of less note, are unmarked by the cross lines so characteristic of the striped fibres ; moreover, the apparent fibres are in reality made up of elongated contractile cells cemented together by some kind of uniting medium. Microscopically two kinds of involuntary muscular tissue are distinguished, viz. the *plain* or *unstriped*, and the *cardiac* tissue ; the latter may be regarded as a form of tissue intermediate between the cross-striated voluntary fibres and the plain involuntary muscular tissue.

PLAIN OR UNSTRIPED MUSCULAR TISSUE.

This, as has just been remarked, is made up of cells, named *contractile fibre-cells*, which were first distinguished as the true elements of the tissue by Kölliker. The cells may form fibrous bundles, and strata, or may be less regularly arranged, and the tissue occurs either almost pure or mixed with other tissues in varying proportion. The cells are of an elongated fusiform shape (figs. 130 and 131), usually pointed at the ends. They are generally roundish or prismatic in transverse section, but are sometimes more flattened. The cells vary greatly in length according to the part or organ in which they are found. Some occur which are cleft or forked at one or both ends. Their substance is finely vacuolated and exhibits also a faint longitudinal fibrillation. It is doubly refracting. Each cell has a nucleus (*a, a*), rarely more than one, which is always elongated and either oval or rod-shaped. Towards each end of the nucleus the substance of the cell usually contains a few distinct granules arranged in linear series.

The nucleus shows the usual structure, having an intranuclear net work (fig. 130, A). The involuntary fibre-cells can be shown to possess an exceedingly delicate homogeneous sheath or envelope (fig. 130, B), and like the sarcolemma of voluntary muscular fibres, this sheath is apt to be wrinkled when the fibre is contracted, so that an indistinct appearance of

striation may thus be produced. The cells are united by a small amount of intercellular cementing substance which becomes stained by nitrate of silver.

They are generally collected into larger and smaller fasciculi, which in many cases cross one another and interlace. The fasciculi are attached at their ends by connective tissue to the membranous and firmer parts where they occur. In some cases the attachment of the plain muscular cells takes place by means of elastic fibres which bifurcate at the end of

Fig. 130.

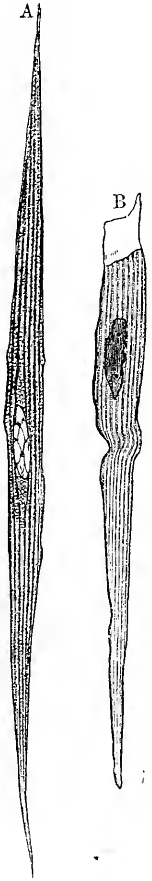

Fig. 131.

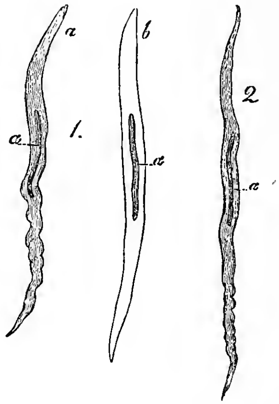

Fig. 130.—Muscular fibre-cells from the muscular coat of the small intestine, highly magnified (E. A. S.).

A. A complete cell, showing the nucleus with intranuclear network, and the longitudinal fibrillation of the cell-substance, with finely vacuolated protoplasm between the fibrils.

B. A cell broken in the process of isolation ; the delicate enveloping membrane projects at the broken end a little beyond the substance of the cell (B is from a drawing by Mr. R. Boxall).

Fig. 131.—Muscular fibre-cells from human arteries, magnified 350 diameters (Kölliker).

a, *a*, nucleus ; *b*, a cell treated with acetic acid.

the muscular cell. The two branches extend along either side of this and are firmly attached to it. In other cases again, according to Watney, the attachment may take place through the medium of connective tissue corpuscles, the branches of which embrace the muscular cell in like manner.

Distribution.—The plain muscular tissue is for the most part disposed in the coats of the membranous viscera. It is met with in the lower half of the gullet, the stomach, and the whole intestinal canal ; that is,

both in the muscular coat of the alimentary canal, and also as a layer in the tissue of the mucous membrane, and in the villi ; in the trachea and bronchial tubes, in the bladder and ureters, and the ducts of the larger glands generally, in the uterus and its appendages, in the corpora cavernosa of both sexes, in the prostate gland, in the spleen, in the muscle of Müller at the back of the orbit, and in the ciliary muscle and iris. The middle coat of the arteries, the coats of many veins and those of the larger lymphatics contain plain muscular tissue. In the skin it is present in the ducts of the sweat glands, in the form of minute muscles attached to the hair-follicles, and in the dartos or subcutaneous tissue of the scrotum. Numerous nerves, chiefly of the pale variety, are supplied to this tissue; before their ultimate distribution they very frequently come into connection with microscopic ganglia. The tissue receives blood-vessels but these are far fewer in proportion than those of voluntary muscle. In some situations, as in the wall of the stomach and intestine, abundant lymphatic plexuses are found in close relation to the muscular layers.

Fig. 132.

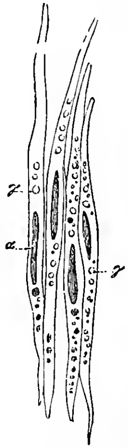

Fig. 132.—Muscular fibre-cells from the uterus three weeks after delivery, treated with acetic acid, magnified 350 diameters (Kölliker).

a, nuclei ; γ, fat-granules.

Development.—The elements of the plain or unstriped muscular tissue are derived from embryonic nucleated cells, consisting of the usual granular protoplasmic substance. These cells become lengthened out, pointed at the ends, and flattened, with elongation of the nucleus, whilst their substance becomes more uniform in aspect, and acquires its permanent condition and characteristic properties.

The great increase in the muscular tissue of the uterus during gestation takes place both by elongation and thickening of the pre-existing fibre-cells of which that non-striated tissue consists, and it is said also by the development of new muscular fibre-cells from small, nucleated, granular cells lying in the tissue. In the shrinking of the uterus after parturition the fibre-cells diminish to their previous size ; many of them become filled with fat granules (fig. 132), and eventually many are doubtless removed by absorption.

Fig. 133.

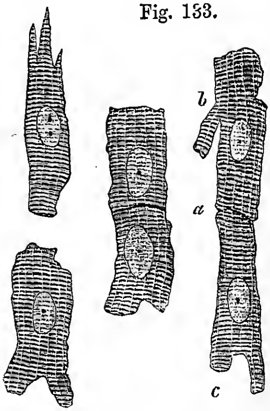

Fig. 133.—Six muscular fibre-cells from the heart, magnified 425 diameters. (E. A. S.) *a*, line of junction between two cells ; *b*, *c*, branching of cells. From a drawing by Mr. J. E. Neale.

CARDIAC MUSCULAR TISSUE.

The fibres of the heart (figs. 133, 134) differ remarkably from those of involuntary muscular organs in general, inasmuch as they present transverse striæ. The striæ, however, are less strongly marked, and less regular, and the fibres are smaller in diameter than in the voluntary

muscles. They differ also from these in being made up of distinct quadrangular cells (fig. 133) joined end to end and often presenting a branched or forked appearance near one extremity (*c*). Each cell has a single clear

Fig. 134.

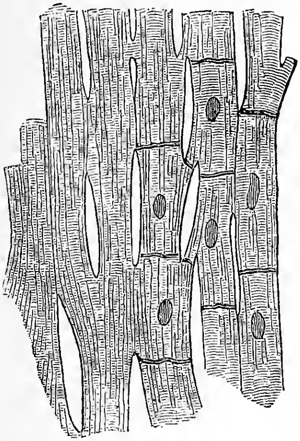

Fig. 134.—MUSCULAR FIBRES FROM THE HEART, MAGNIFIED, SHOWING THEIR CROSS STRIÆ, DIVISIONS, AND JUNCTIONS (Schweigger-Seidel).

The nuclei and cell-junctions are only represented on the right-hand side of the figure.

oval nucleus situate near the centre ; occasionally two nuclei are seen. The cell substance is striated longitudinally as well as transversely, its substance appearing to be composed of a number of parallel columns or fibrils, which on transverse section are seen as small polygonal areas. An investing membrane or sarcolemma has not hitherto been proved to exist on these fibres.

The muscular fibres of the heart freely divide and anastomose (fig. 134), the junctions with neighbouring fibres being effected by the medium of the cell-offsets above noticed.

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NERVOUS SYSTEM.

The nervous system consists of a *central part*, or rather a series of connected *central organs*, named the *cerebro-spinal axis*, or *cerebro-spinal centre;* and of the *nerves*, which have the form of cords connected by one extremity with the cerebro-spinal centre, and extending from thence through the body to the muscles, sensible parts, and other organs placed in functional relation with them. The nerves form the medium of communication between these distant parts and the centre. One class of nervous fibres, termed *afferent* or *centripetal*, conduct impressions towards the centre,—another, the *efferent* or *centrifugal*, carry motorial stimuli from the centre to the moving organs.

Besides the cerebro-spinal centre and the nervous cords, the nervous system comprehends also certain bodies named *ganglia*, which are connected with the nerves in various situations. These bodies, though of much smaller size and less complex nature than the brain, agree, in some respects, with that organ in their elementary structure, and to a certain extent also in their relation to the nervous fibres with which they are connected; and this correspondence becomes even more apparent in the nervous system of the lower members of the animal series.

The nerves are divided into the *cerebro-spinal*, and the *sympathetic* or *ganglionic* nerves. The former are distributed principally to the skin, the organs of the senses, and other parts endowed with manifest sensibility, and to muscles placed more or less under the control of the will. They are attached in pairs to the cerebro-spinal axis, and like the parts which they supply are, with few exceptions, remarkably symmetrical on the two sides of the body. The sympathetic or ganglionic nerves, on the other hand, are destined chiefly for the viscera and blood-vessels, of which the motions are involuntary, and the natural sensibility is obtuse. They differ also from the cerebro-spinal nerves in having generally a greyish or reddish colour, in their less symmetrical arrangement, and especially in the circumstance that the ganglia connected with them are much more numerous and more widely distributed. Branches of communication pass from the spinal and several of the cerebral nerves at a short distance from their roots, to join the sympathetic, and in these communications the two systems of nerves mutually give and receive nervous fibres; so that parts supplied by the sympathetic may be also in nervous connection with the cerebro-spinal centre.

The nervous system is made up of a substance proper and peculiar to it, with inclosing membranes, nutrient blood-vessels and supporting connective tissue. The *nervous substance* has been long distinguished into two kinds, obviously differing from each other in colour, and therefore named the *white*, and the *grey* or *cineritious*.

When subjected to the microscope, the nervous substance is seen to consist of two different structural elements, viz., *fibres* and *cells*. The fibres are found universally in the nervous cords, and they also constitute the greater part of the nervous centres: the cells on the other hand are confined in a great measure to the cerebro-spinal centre and the ganglia, and do not exist generally in the nerves properly so called, although they have been found at the terminations of some of the nerves of special sense, and also interposed here and there among the fibres of particular

nerves; they are contained in the grey portion of the brain and spinal cord, and in the ganglia.

NERVE-FIBRES.

Two kinds of nerve-fibres are met with in the body, differing from one another both in their microscopical character and in their more obvious aspect: those of the one kind have received the name of *white* fibres, on account of the appearance which they present when collected in considerable numbers, as in the nerve trunks or white matter of the nerve centres, the others being denominated *grey* fibres.

Fig. 135.

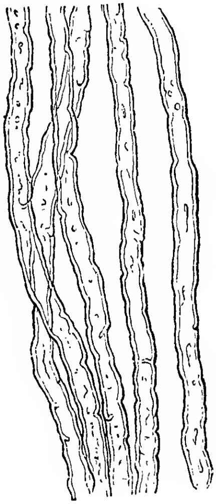


Fig. 136.

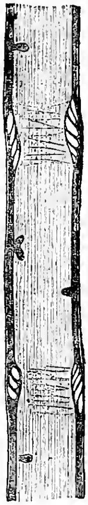


Fig. 135.—White or medullated nerve-fibres, showing the sinuous outline and double contours (after Bidder and Volkmann).

Fig. 136.—A small part of a medullated fibre highly magnified (E. A. S.).

The fibre looks in optical section like a tube—hence the term tubular, formerly applied to these fibres. Two partial breaches of continuity are seen in the medullary sheath, which at these places exhibits a tendency to split into laminæ. The primitive sheath is here and there apparent outside the medullary sheath, and the delicate striæ which are visible in the middle of the fibre probably indicate the fibrillated axis-cylinder.

When examined with the microscope it is found that this difference of aspect depends upon the presence or absence of a peculiar sheath to the fibre, formed of a kind of fatty substance, this fatty or medullary substance, as it is termed, giving a dark double contour to the white fibres (when seen by transmitted light), which is altogether absent from those of the other kind. On account of this the white fibres are also known as the *dark-bordered* or *medullated* fibres, the grey fibres being termed in contradistinction the *pale* or *non-medullated* fibres, or from their discoverer, the *fibres of Remak*.

The **medullated nerve-fibres** form the white part of the brain, spinal cord, and nerves, and give it its white opaque aspect. Viewed singly under the microscope with transmitted light they are transparent, and, as before stated, are characterised by their well-defined even outline and, except the smallest, by their double contour, which gives them a tubular aspect.

Their size differs considerably even in the same nerve, but much more in different parts of the nervous system; some being as small as the $\frac{1}{12000}$th and others upwards of the $\frac{1}{1500}$th of an inch in diameter; moreover, the same fibre may change its size in different parts of its course, and it is generally smaller at its central and peripheral ends.

Fig. 137.

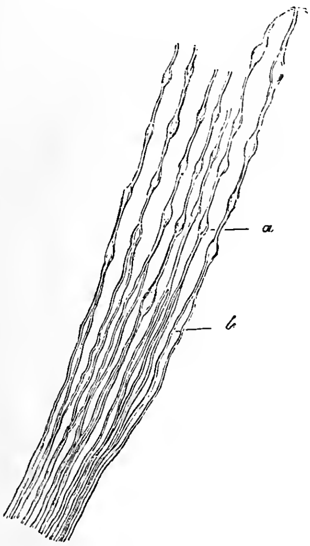


Fig. 138.

B.

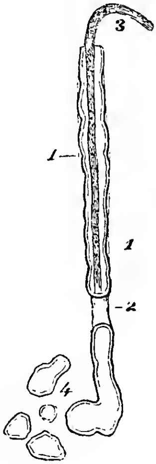


Fig. 137.—Varicose medullated fibres from the root of a spinal nerve (from Valentin).

Fig. 138.—B. Diagram to show the parts of a medullated fibre, viz., 1, 1, *outer* or *primitive sheath* enclosing the doubly contoured *white substance* or *medullary sheath*. 2, a part where the white substance is interrupted the outer sheath remaining. 3, *axis cylinder* projecting beyond the broken end of the tube. 4, part of the contents of the tube escaped.

Many of the medullated nerve-fibres appear dilated or swollen out at short distances along their length, and contracted in the intervals between the dilated parts. These fibres, however, are naturally cylindrical like the rest, and continue so while they remain undisturbed in their place; and the varicose character is occasioned by pressure or traction during the manipulation, which causes the soft matter to accumulate at certain points, whilst it is drawn out and attenuated at others (fig. 137). The fibres in which this is most apt to occur are usually of small size, ranging from $\frac{1}{12000}$th to $\frac{1}{3600}$th of an inch in diameter; and when a

very small fibre is thus affected, the varicosities appear like a string of globules held together by a fine transparent thread.

The medullated fibres are composed for the most part of three distinct structures, viz., an axial fibre (the cylinder-axis of Purkinje), enclosed within two sheaths, one of these being the medullary sheath already mentioned, and the other a delicate membranous tube outside of all, termed the nucleated sheath of Schwann, the primitive sheath, or simply, the outer sheath. But there are medullated fibres in which the primitive sheath is absent, and other fibres and prolongations of fibres in which there is no sheath whatever to the axis-cylinder. But the latter is always present, and is indeed the chief functional constituent of the nerve-fibre. The several parts of which the nerve-fibre is composed may now be described in detail.

Axis-Cylinder.—The essential part of every nerve-fibre, is a pale and somewhat indistinct strand, which runs in the axis of the fibre and is termed the *axis-band*, *axial-fibre*, or more commonly the *axis-cylinder* (fig. 138, 3 ; and 139, *c*). This essential part is usually inclosed,

Fig. 139.

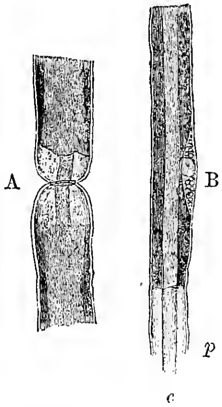


Fig. 140.

Fig. 139.—Two portions of medullated nerve fibres, after treatment with osmic acid, showing the axis-cylinder, and the medullary and primitive sheaths (Key and Retzius).

A. Node of Ranvier. B. Middle of an internode with nucleus.

c, axis-cylinder, projecting at the broken end ; *p*, primitive sheath within which the medullary sheath, which is stained dark by the osmic acid, is somewhat retracted.

Fig. 140.—Part of an axis-cylinder, highly magnified, showing the varicose fibrils composing it (Max Schultze).

as just mentioned, in one or more sheaths, but these are not always present, especially at the origin and termination of a nerve-fibre ; and even in the course of the fibre they may be interrupted at intervals. The central axis, on the other hand, undergoes no interruption along the

whole course of the nerve, from the nerve-centre to the peripheral distribution. It appears further to be clearly established that the axial fibre of a nerve is in nearly every case a direct prolongation of a branch of a nerve-cell situated in one part or another of the nerve-centre. It is therefore to be looked upon in the light of a far-extending cell process; and the study of the development of the nerve-fibre affords a direct confirmation of this view of its nature.

In the fresh state, and under high powers of the microscope, the axis-cylinder presents an appearance of longitudinal striation, indicating a fibrillar structure (fig. 140); and at the termination of the nerves it may often be seen to separate into a number of exquisitely fine filaments or fibrils. These, the *primitive fibrillæ* of Max Schultze, are embedded in a homogeneous or finely-granular material, and may with some reason be regarded as constituting the essential or conducting part of the axis-cylinder, and therefore of the nerve: at least, it frequently happens that they form the only portion of the nerve-fibre that is prolonged to the ultimate termination. The fibrils often exhibit minute varicosities which are highly characteristic in appearance.

The axis-cylinder appears to be invested with a very delicate structureless sheath.

It was shown by Fromann that after treatment with nitrate of silver and subsequent exposure to the light the axis-cylinder becomes stained in such a manner as to exhibit a distinct cross-striated aspect, but it is not known whether this depends upon any structural feature of the fibre or not.

It is not always easy to distinguish the axis-cylinder in the medullated fibres when they are examined in the fresh condition, but it can generally be made manifest by staining the nerve with carmine or hæmatoxylin. In a transverse section of a nerve thus stained the axis-cylinders appear in the form of round darkly coloured dots in the centre of the fibres.

Medullary Sheath.—The substance of the medullary sheath (which was termed the white substance by Schwann on account of its presence being the chief cause of the whiteness of the nerves), undergoes peculiar changes on exposure of the nerve to the action of water and other fluids, so that the outline of the fibre is often rendered uneven; round and irregular spots appear at various points, the medullary sheath acquiring eventually a confusedly curdled aspect.

The thickness of this sheath varies within wide limits, and indeed this is the chief cause of the variation in size of the medullated nerve-fibres, although the axis-cylinder may also vary in diameter to a considerable extent. In some fibres, the medullary substance forms an exceedingly thin layer, so as to be scarcely distinguishable except by the darker outline which it imparts to the fibre, or it may only occur in parts, these alternating irregularly with other parts in which there is a complete absence of white substance. Such fibres, which are very common in some parts of the sympathetic system (fig. 152, *m, m*), may be regarded as transitional between the white and the grey fibres.

Nodes and internodes of Ranvier.—It was shown by Ranvier, that there constantly occur in the peripheral medullated nerve-fibres breaks in the continuity of the white substance, which succeed one another at regular intervals along the course of the nerves; and give the fibres the appearance of being constricted at these places. The

constrictions or *nodes of Ranvier*, as they may conveniently be termed, divide the fibre into a series of *internodes* of nearly equal length. The segmentation is readily made apparent by the action of a

Fig. 141.

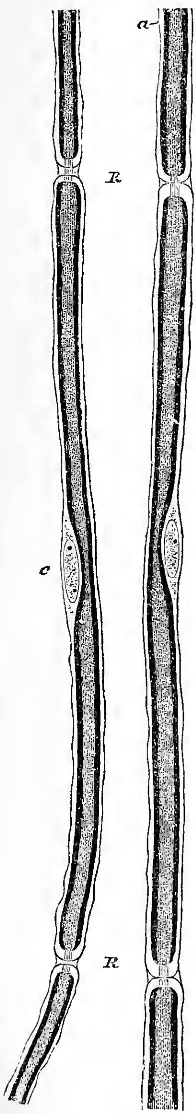


Fig. 141.—PORTIONS OF TWO NERVE-FIBRES STAINED WITH OSMIC ACID (FROM A YOUNG RABBIT). 425 DIAMETERS (E. A. S.).

R, R. Nodes of Ranvier, with axis-cylinder passing through. *a*, Primitive sheath of the nerve. *c*, Opposite the middle of the segment indicates the nucleus and protoplasm lying between the primitive sheath and the medullary sheath. In A the nodes are wider, and the intersegmental substance more apparent than in B. (From a drawing by Mr. J. E. Neale.)

solution of osmic acid, which leaves the nodes (fig. 141, R, R; fig. 142, E) almost colourless, while the medullary sheath, or white substance of Schwann, becomes stained of an inky black colour.

The white substance of the medullary sheath is often found to have shrunk somewhat in the neighbourhood of a node (fig. 139, A), and it can then be seen that there is present, in addition to it, a clear or finely granular stroma, which has become evident in consequence of retraction of the fatty substance which normally pervaded it.

The outer membranous sheath of the fibre appears to be continued over the nodes, for when a medullated fibre is examined in water and the substance of the medullary sheath exudes from the cut ends of the nerve-fibres, it is found that the place of that which thus escapes is taken by the white substance from the next internode; and this substance may be seen to flow past the constrictions of Ranvier without escaping at those points. Outside the primitive sheath the internodes are united by a disc of cementing substance—the "constricting band" of Ranvier — which, like intercellular substance elsewhere, becomes stained by nitrate of silver. The last-named reagent stains also the axis-cylinder in the neighbourhood of the node, so that the fibres after this treatment appear marked with little crosses (fig. 151); the transverse limb of the cross being due to the ring of intersegmental substance, the longitudinal to the axis-cylinder. Many other fluids stain the axis-cylinder at the nodes only, being prevented from reaching it elsewhere owing to the presence of the fatty matter in the surrounding medullary sheath.

Engelmann argues in favour of a discontinuity of the axis-cylinder (as well as of the medullary sheath) at the nodes of Ranvier, basing his argument partly on the immediate degeneration which results when a nerve-fibre is cut, partly on appearances obtained after a

certain method of treatment with nitrate of silver, the dark deposit characteristic of inter-cellular substance traversing, according to his account, the

Fig. 142.—MEDULLATED NERVE-FIBRE TREATED WITH OSMIC ACID (Key and Retzius.)

A node of Ranvier (E) and a nucleus (K) is represented. The medullary sheath appears broken up into a number of segments with conical or funnel-shaped ends fitting into one another.

Fig. 142.

thickness of the axis-cylinder at the nodes. But such a view would require far stronger evidence than has yet been brought forward before it can be accepted, for it is opposed to the best ascertained facts with regard to the development and regeneration of the axis-cylinder.

In the middle of each internode an oval nucleus lies embedded in the medullary sheath (figs. 139, B, 141, *c*, 142, K), these nuclei will be described with the primitive sheath.

Medullary segments.—Other breaks of continuity are seen in the medullary sheath (fig. 136) which are of an entirely different nature from the nodes of Ranvier; indeed it is somewhat uncertain how far they correspond to a pre-existent structure in the fibre. In consequence of their presence the medullary sheath almost constantly appears as if made up of a number of small cylindrical segments with either conical or funnel-shaped ends which fit in with one another in the alternate segments (fig. 142), and the parts in question have since been frequently described as integral constituents of the medullary sheath (Lantermann, Schmidt and others). It is easy to convince oneself of the reality of the appearances here mentioned, but it is far less easy to be certain that they are not artificial productions. Against the view of their existence in the natural condition it is to be noted that they are extremely variable in number and in size in a given length, even of the same nerve-fibre, that they appear to become increased in number if the nerve-fibre have been subjected to much manipulation, that they have no constant relation, so far as can be made out, to the other parts of the medullated fibre, and that, according to the testimony of several careful observers, they are not to be seen in the nerve-fibres of the living animal, unless these have been subjected to an abnormal amount of traction or other mechanical injury. This last assertion is denied, however, by others, who maintain the pre-existence of the medullary segments, and describe them and the oblique clefts which separate them as definite parts of the sheath.

Rod-like and reticular structures in the medullary sheath.—It was shown by McCarthy that after a nerve has been hardened with chromate of ammonium (picric acid is still better adapted for the purpose) the medullary sheath appears pervaded with minute rod-like structures which pass radially between the axis-cylinder and the primitive sheath in such a manner as to give the cross-section of a nerve-fibre the appearance of a wheel. The rods stain with carmine and hæmatoxylin, which do not colour the fatty substance of the medullary sheath. In nerves stained with osmic acid (in which these structures were first detected by Lantermann) they are far less easily seen, in consequence of the dark colouration of the fatty substance in which they are embedded. The rods are probably not distinct from one another, but in reality united laterally so

as to form a close network, for if the nerve be first placed in strong alcohol and then subjected to the action of staining fluids it will be found that the rod-like structures are no longer visible but the medullary sheath appears pervaded instead by a finely reticular structure. The network thus obtained is considered by Kühne and Ewald, who first drew attention to it, to be chemically of a horny nature, on account of the resistance it offers to reagents, and especially to digestive ferments; and they further describe it as continuous with two exceedingly delicate membranes of a similar nature one immediately investing the axis-cylinder and the other lining the primitive sheath. Ranvier on the other hand describes the medullary sheath as bounded both towards the axis-cylinder and towards the primitive sheath by fine layers of protoplasm, and he regards these as being connected with one another by protoplasmic septa, which lie in the intervals between the conico-cylindrical segments of the medullary sheath.

It will be seen from the above that there is still much diversity of opinion with regard to the minute structure of the medullary sheath of the nerves. As to its chemical composition the white substance or *myelin*, consists chiefly of protagon (or of its derivatives lecithin and neurin) together with cholesterin and one or two other substances in less amount. When escaped from the nerve-fibres it forms drops either rounded or irregular in shape, which always show the double contour which is so characteristic of the medullated nerve-fibres, the appearance being due to the peculiar manner in which myelin refracts the light. In contact with water it combines with that fluid, and as a result of the imbibition the myelin-drops undergo a considerable increase in bulk, accompanied by remarkable changes of form, often growing out into tube-like filaments for a considerable distance into the fluid. In this behaviour myelin is not peculiar but resembles certain other substances of a fatty and resinous nature.

Sheath of Schwann, Outer or **Primitive Sheath.**—The nucleated sheath of Schwann forms the outermost covering of the white nerve-fibres. It presents the appearance of a delicate homogeneous membrane with nuclei disposed at intervals along its inner surface. As already mentioned these nuclei bear a definite relation to the constrictions or nodes of Ranvier, for they lie about midway between the nodes, only one nucleus being found in each internode (fig. 141). The nuclei are oval and sometimes flattened, they usually lie in a depression of the medullary sheath, and at each end of the nucleus, especially in young nerves, there is a small amount of granular protoplasm which may spread for a short distance between the primitive and the medullary sheath. The primitive sheath turns in at the nodes and closely surrounds the axis-cylinder as this passes from one segment to the other.

So long as the primitive sheath is accurately filled by the contained medullary substance its outline can seldom be distinguished, but sometimes, when the white substance separates at various points from the inside of the tube, the contour of the fibre becomes indented and irregular, and then the membrane of the tube may, in favourable circumstances, be discerned as an extremely faint line, running outside the deeply shaded border formed by the white substance.

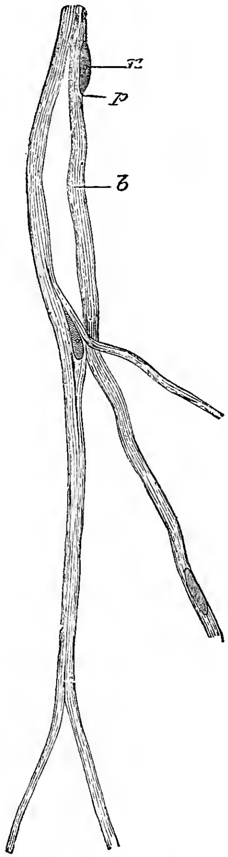
In the white fibres of the brain and spinal cord the nucleated sheath is absent, and these are only invested by a medullary sheath in which nodes of Ranvier have not been detected. In consequence of the absence of the comparatively tough primitive sheath the fibres from these situations cannot be isolated for any distance without rupture, and

it is found that for the same reason the medullary sheath readily breaks away from the axis-cylinder, so that this is thus left bare.

Fig. 143.—PORTION OF THE NETWORK OF FIBRES OF REMAK FROM THE PNEUMOGASTRIC OF THE DOG (Ranvier).

n, nucleus; *p*, protoplasm surrounding it; *b*, striation caused by fibrils.

Fig. 143.



Pale or non-medullated fibres; Fibres of Remak.—These occur principally in branches of the sympathetic nerve, but they are found also in greate or less amount in the cerebro-spinal nerves. They are exceedingly pale, faintly striated fibres of varying size, which exhibit nuclei at frequent intervals. The nuclei are applied to the surface of the fibre, and, according to the generally received account, belong to a delicate homogeneous sheath, like the primitive sheath of the medullated fibre. It must be admitted, however, with Ranvier that it is difficult or impossible to exhibit the sheath, and if this is the case, the nuclei must be regarded as embedded in the peripheral layer of the fibre itself, and as belonging to this. The fibres in question differ also from the medullated fibres in being frequently branched and united with neighbouring fibres, so as to form a network along their course; a condition which is never found in the course of the medullated nerves. The branches of the olfactory nerve consist wholly of pale fibres, but these are different from the ordinary pale fibres in being provided with a distinct nucleated sheath.

NERVE-CELLS.

These are found in the grey matter of the brain and spinal cord and in the ganglia; they exist also in some of the nerves of special sense near their terminations, and occur here and there in the course of certain other nerves. They are often named ganglion-cells.

In shape, nerve-cells vary greatly. Thus they may be spheroidal or ovoidal with a general even outline, or they may be of an angular or irregular figure, and it is found that the nerve-cells have a characteristic shape in certain parts of the nervous system. For example, the cells from the spinal ganglia are generally of a rounded shape (see fig. 156, p. 157), those from the sympathetic ganglia more angular (fig. 155), those from the grey matter of the spinal cord of an exceedingly irregular form, and provided with numerous branching processes (fig.

144); those from the cerebral convolutions conical, those from a particular layer of the grey matter of the cerebellum, flask-or retort-shaped (fig. 145), and so on. The cells which are situated in the course of peripheral nerves are often somewhat spindle-shaped, the two poles of the spindle being prolonged into nerve fibres.

Fig. 144.

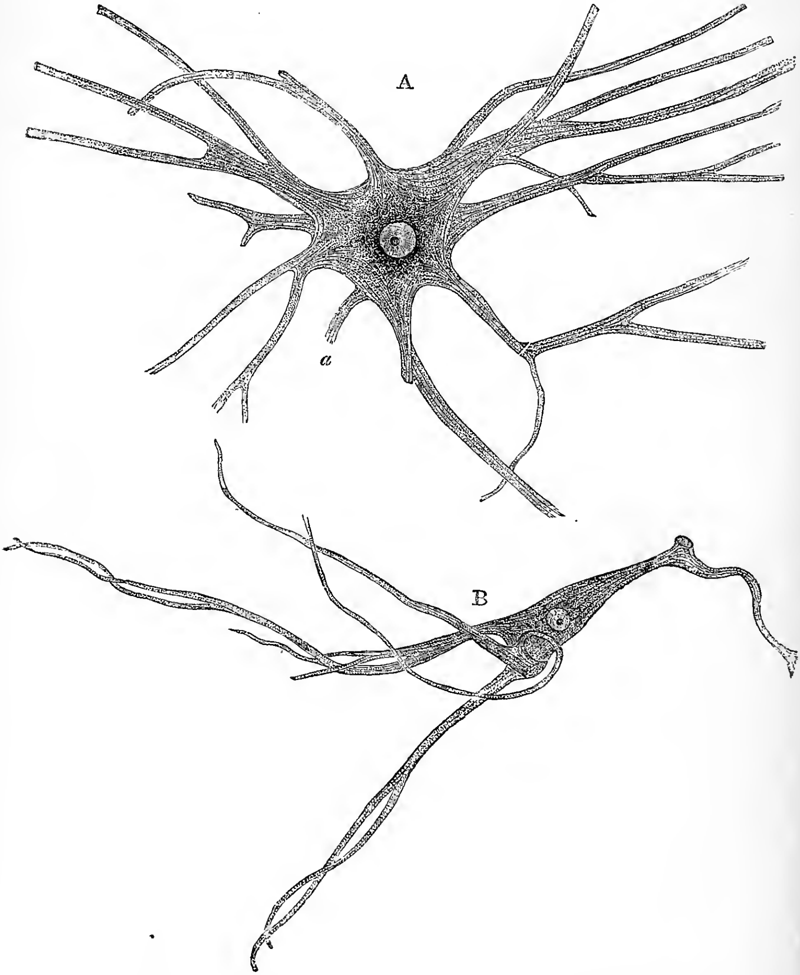


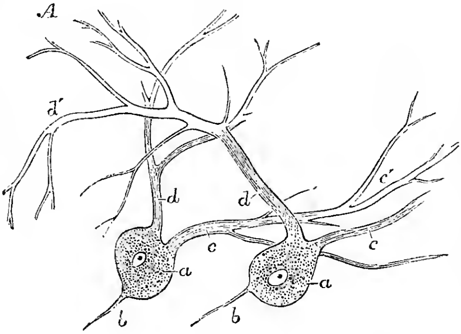
Fig. 144.—Two nerve-cells from the spinal cord of the ox, isolated after maceration in very dilute chromic acid. Magnified 175 diameters. (E.A.S.)

Each cell has a well-defined, clear, round nucleus, and a large nucleolus. The cell processes are seen to be finely fibrillated, the fibrils passing from one process into another through the body of the cell. A, from the anterior cornu of grey matter, large and stellate, with numerous processes; *a*, axis-cylinder process broken a short distance from the cell. B, probably from the posterior cornu, more fusiform in shape and apparently destitute of an axis-cylinder process.

Nerve-cells vary much in size as well as in shape. Many of the nerve-cells in the body are very large, but there are others which are quite small, and consist of little more than nuclei. The latter are especially abundant in the deeper part of the grey matter of the cerebellum, where they form what is known as the granule-layer.

Fig. 145.—Two nerve-cells from the cortical grey matter of the cerebellum. Magnified 260 diameters (Kölliker).

Fig. 145.

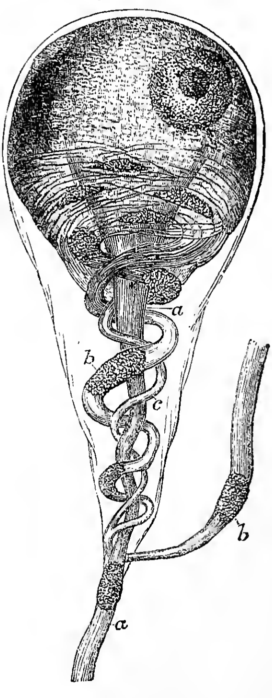


Structure. — The nucleus of a nerve-cell (fig. 144) is usually a large clear round vesicle containing a very distinct highly refracting nucleolus, and, in some cases, an intranuclear net-work. The cell-substance is finely granular or punctated, sometimes indistinctly striated. It frequently has a brownish-red tinge, but besides this, cells are often to be seen which contain very distinct brown or yellow coloured patches caused by an accumulation of pigment granules. The colour is deeper in adult age than in infancy.

Fig. 146.—Ganglion-cell of a frog, highly magnified (Beale).

a,a, straight fibre ; *b, b*, coiled fibre ; *c*, smaller one joining it.

Fig. 146.



Every nerve-cell has one or more processes, and the cells are often named according to the number of processes they possess, uni-, bi-, and multi-polar ; terms not perhaps well-chosen, but rendered current by use. A fibrillation similar to that in the axis-cylinder of a nerve-fibre is visible in the cell-processes, and it may also be traced passing from them into the body of the cell and even through this from one process into another. Some affirm that they have been able to trace a connection of these fibrils with the nucleus of the cell, but this is at present doubtful.

Nerve-cells which are entirely destitute of processes have sometimes been described. It is possible that such may exist, but there is always a probability that these may be cells, the processes of which have become broken away during the manipulation required for isolation.

It has been shown that many cells have at least one of their processes

prolonged as a nerve-fibre (axis-cylinder process). In the case of the bi-polar cells, especially those of a spindle-shape with a process from either end, both these processes are prolonged as nerve-fibres (fig. 154): from another point of view the cell might be looked upon as a nucleated enlargement interpolated in the course of the fibre.

Fig. 147.

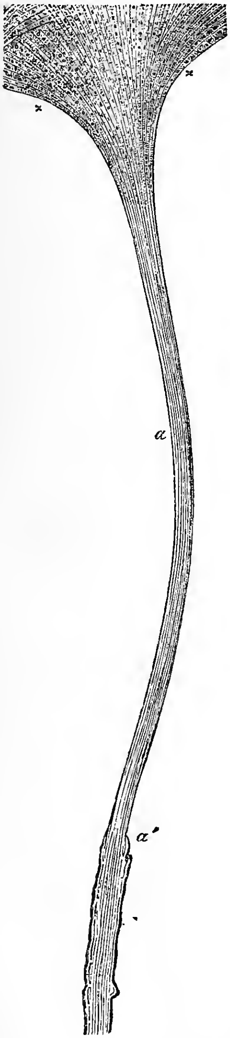


Fig. 147.—Axis-cylinder process of a nerve-cell (M. Schultze).

×, ×, Portion of nerve-cell from spinal cord of ox, with axis-cylinder process, *a*, coming off from it and acquiring at *a'* a medullary sheath. Highly magnified.

In other bi-polar cells in which the processes come off on the same side of the cell, the latter often has a pyriform shape (fig. 146), the fibres being prolonged from the stalk of the pear and the nucleus of the cell being placed in the larger end. As was shown by Beale, a peculiar arrangement of the two fibres which are thus prolonged from these pear-shaped cells is found, the one being generally coiled spirally round the other for a certain distance, after which the fibres separate and take opposite directions. Cells of this kind are met with occasionally in the sympathetic ganglia both of the frog (where they were first discovered by Beale) and of the mammal.

In multi-polar cells either one or more of the cell-processes may be prolonged into nerve-fibres. In the large ramified nerve-cells of the anterior cornu of the spinal cord only one of the many processes is prolonged into a nerve-fibre. This is known as the axis-cylinder process of Deiters (fig. 145, *a*, and fig. 147), and is distinguished from the other processes of the cell by being unbranched and of a somewhat clearer and more evenly fibrillated appearance than the other processes, which branch again and again, becoming finer as they proceed, until they are eventually lost to sight in the grey matter. Other multi-polar cells, many of those in the sympathetic system for instance, possess several nerve-fibre processes (fig. 155).

Sometimes these axis-cylinder processes of a nerve-cell, especially those in the sympathetic, are continued along their whole course as pale nerve-fibres. But in many cases, at a short distance from the body of the cell, they acquire a medullary sheath and become in fact medullated nerve-fibres (fig. 147, *a'*). In the bi-polar cells (those at least of a pyriform shape), the one fibre may be prolonged as a pale fibre, the other as a medullated fibre. In other instances both fibres may become dark-bordered or both continue as pale fibres. In the uni-polar cells of the

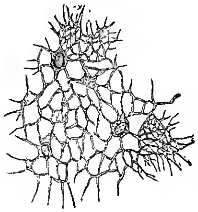
ganglia upon the posterior roots of the spinal nerves, and in some other situations the single process (which may be much convoluted near the cell and soon acquires a medullary sheath) bifurcates after a longer or shorter course, and its two branches are eventually prolonged in opposite directions along the nerve (fig. 156).

The nerve-cells in the brain and spinal cord resemble the nerve-fibres in the same parts in being destitute of any nucleated sheath, but in the ganglia each nerve-cell is inclosed in a membranous capsule, having nuclei on its inner surface and apparently continuous with the nucleated sheath of the nerve-fibre or fibres with which the cell is connected (fig. 155).

Sustentacular tissue of the nerve-centres; reticulum, neuroglia.—In the grey matter of the cerebro-spinal centre, the nerve-cells appear at first sight as if imbedded in a sort of matrix of granular substance, interposed between them in greater or less quantity, and very generally traversed by nerve-fibres. But it is very probable that the appearance of granular or molecular matter results from a confused interlacement of fine fibrils and especially of the fine ramifications of nerve-cells: or from the crushing and breaking down of such fibres in the process of examination.

Fig. 148.—Part of the reticulum from the spinal cord (Kölliker). Magnified 350 diameters.

Fig. 148.



The supporting substance which is met with in the white matter of the brain and spinal cord between the nerve-fibres also looks in section like a network, although rather more open than that in the grey matter. It was supposed by Kölliker to be a form of retiform tissue and to be composed of branched cells; accordingly he named it the *reticulum* of the nervous centres, but the term *neuroglia* which was proposed by Virchow has been more generally adopted. It is not, however, composed of cells, although these may occur in it, but it is rather of the nature of an intercellular substance which occupies the interstices between the nerve-fibres. The cells which are here and there found in it are flattened and resemble small connective tissue corpuscles, and the neuroglia of the nerve-centres has generally been regarded as consisting of connective tissue ground-substance, especially since in many places it appears fibrillated. Moreover, it is apparently in continuity with the connective tissue septa which pass into the substance of the spinal cord and brain from the investing sheath of pia mater. In the nerve-trunks, as we shall immediately see, the supporting tissue between the nerve-fibres, which also in section has the appearance of a network, is evidently composed of delicate connective tissue. By some authorities, however, the neuroglia is regarded as of the same nature as the intercellular substance of an epithelium, and the cells in it are considered to be analogous with the branched migratory cells which are sometimes found in the intercellular substance of a stratified epithelium.

Kühne and Ewald for similar reasons to those mentioned in speaking of the network of the medullated sheath of the nerve-fibre, have concluded that the

fine interlacement of fibres in the nerve-centres is also of a horny nature, and they have accordingly termed it the "horny framework."

Such being the structural elements of the nervous substance, we have next to consider the arrangement of the cells and fibres in the ganglia and nerves which they contribute to form; the intimate structure of the brain and spinal cord being treated of in a subsequent part of this work.

CONSTRUCTION OF THE NERVES OR NERVOUS CORDS.

The nerves are formed of the nerve-fibres already described, collected together and bound up in sheaths of connective tissue. A variable number of fibres inclosed in a tubular sheath forms a slender round cord

Fig. 149.

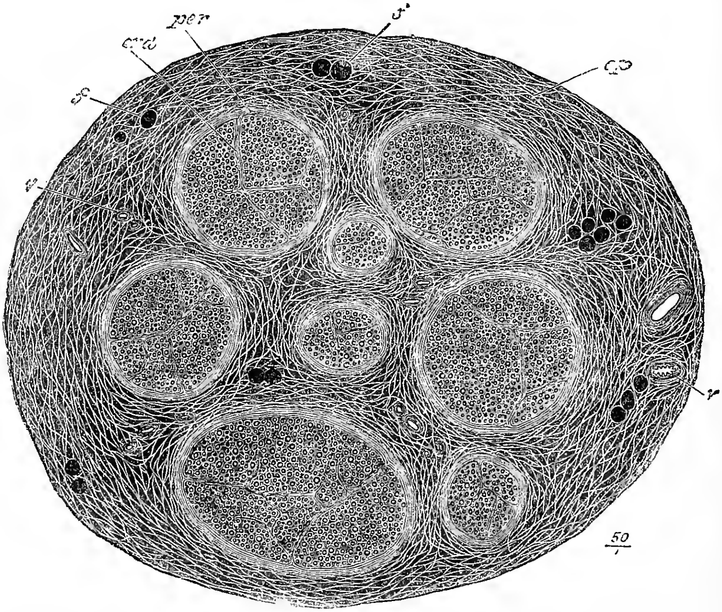


Fig. 149.—SECTION OF THE INTERNAL SAPHENOUS NERVE (HUMAN), MADE AFTER BEING STAINED IN OSMIC ACID AND SUBSEQUENTLY HARDENED IN ALCOHOL. DRAWN AS SEEN UNDER A VERY LOW MAGNIFYING POWER. (E. A. S.)

Ep, epineurium, or general sheath of the nerve, consisting of connective tissue bundles of variable size separated by cleft-like areolæ, which appear as a network of clear lines, with here and there fat-cells *f f*, and blood-vessels *v* : *per* funiculus enclosed in its lamellated connective tissue sheath (perineurium,) ; *end*, interior of funiculus, showing the cut ends of the medullated nerve-fibres, which are imbedded in the connective tissue within the funiculus (endoneurium). The fat-cells and the nerve-fibres are darkly stained by the osmic acid, but the connective tissue of the nerve is only slightly stained.

of no determinate size, usually named a *funiculus;* if a nerve be small it may consist of but one such cord, but in larger nerves several funiculi are united together into one or more bundles, which, being wrapped up in a common membranous covering, constitute the nerve (fig. 149).

Accordingly, in dissecting a nerve, we first come to an outward covering, formed of connective tissue, often so strong and dense that it might well be called fibrous. From this common sheath we trace connective tissue bundles passing between the funiculi, connecting them together as well as conducting and supporting the fine blood-vessels which are distributed to the nerve. But, besides the interposed areolar tissue which connects these smallest cords, each funiculus has a special sheath of its own, as will be immediately noticed.

The common sheath (fig. 149, *ep*) and its sub-divisions consist of connective tissue presenting the usual white and elastic constituent fibres of that texture, the latter being present in considerable proportion: frequently also a little fat is to be found. This common sheath has received the name of *epineurium* (Key and Retzius); it was formerly termed the "cellular sheath" (*vagina cellulosa*).

Fig. 150.

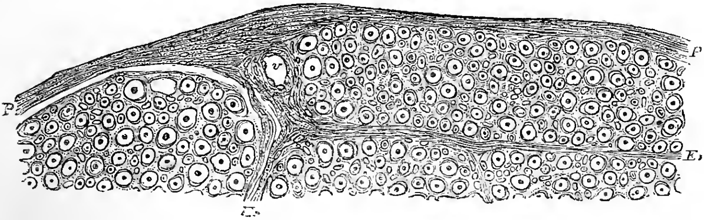


Fig. 150.—Part of a section of one of the funiculi of the sciatic nerve of man. Magnified (after Key and Retzius).

P, Perineurium, consisting of a number of closely arranged lamellæ. *En*, processes from the perineurium, passing into the interior of the funiculus, and becoming continuous with the endoneurium, or delicate connective tissue between the nerve-fibres. The connective tissue fibrils of the endoneurium are seen cut across as fine points, often appearing to ensheath the nerve-fibres with a circle of minute dots (fibril-sheath of Key and Retzius). Numerous nuclei of connective tissue cells are imbedded in the endoneurium; *v*, section of a blood-vessel.

The special sheath of a funiculus, termed the *neurilemma* or *perineurium* (fig. 149, *per.*, 150, P.), is also formed of connective tissue, but is far more distinctly of a lamellar nature, and indeed may be stripped off in the form of a tube from the little bundle of nerve-fibres of which the funiculus consists. The perineurium is not formed of a single lamella but of several, which are separated from one another by interlamellar clefts moistened with lymph. The separation is not everywhere complete, for here and there bundles pass across, connecting the several lamellæ. Moreover, the outermost lamella is joined by connective tissue bundles and laminæ of the epineurium, and the innermost gives off flattened prolongations (fig. 149, *end*), to form imperfect septa between the groups of nerve-fibres within the funiculus.

Although the lamellæ of the perineurium are very thin, each is formed of at least three strata. Thus the main substance of the lamellæ is composed of a connective tissue, in which both white fibres and elastic elements are found, the white fibres having for the most part a transverse disposition. The elastic elements lie in greater abundance nearer the

surfaces of the lamella, and often occur in the form of patches or incomplete membranes of elastic substance (fig. 73, p. 71), as well

Fig. 151.

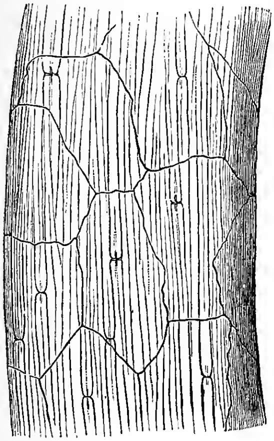


Fig. 151.—A PORTION OF A SMALL NERVE-TRUNK FROM THE THORAX OF A MOUSE, TREATED WITH NITRATE OF SILVER (Ranvier). MAGNIFIED.

Cross markings are seen at the nodes, and the layer of flattened epithelioid cells which covers the surface is also brought into view.

as in the form of a fine network of fibres. On both its surfaces, each lamella is entirely covered with a layer of exceedingly delicate flattened epithelioid cells, which thus serve also to bound the clefts between the lamellæ. The outlines of the cells are brought into view by the silver treatment (fig. 151).

The funiculi of a nerve although not all of one size, are all sufficiently large to be readily seen with the naked eye, and easily dissected out from each other. In a nerve so dissected into its component funiculi, it is seen that these do not run along the nerve as parallel insulated cords, but join together obliquely at short distances as they proceed in their course, the cords resulting from such union dividing in their further progress to form junctions again with collateral cords; so that in fact the funiculi composing a single nervous trunk have an arrangement with respect to each other similar to that which is found to hold in a plexus formed by the branches of different nerves. It must be distinctly understood, however, that in these communications the medullated nerve-fibres do not join together or coalesce. They pass off from one nervous cord to enter another, with whose fibres they become intermixed, and part of them thus intermixed may again pass off to a third funiculus, or go through a series of funiculi and undergo still further intermixture; but throughout all these successive associations (until near the termination of the nerve) the fibres remain individually distinct, like the threads in a rope.

The nerve-fibres are separated from one another, and supported within the funiculus by delicate connective tissue, the fibrils of which run for the most part longitudinally, appearing in section as fine points (fig. 150). This tissue has been distinguished as the *endoneurium* by Key and Retzius. It is continuous with the septa which pass in as above mentioned from the innermost lamella of the perineurium, and it serves to support also the capillary blood-vessels which are distributed to the nerve.

Lying alongside each other, the fibres of a funiculus form a little skein or bundle, which runs in a waving or serpentine manner within its sheath; and the alternate lights and shadows caused by the successive bendings being seen through the sheath, give rise to the appearance of alternate light and dark cross stripes on the funiculi, or even on larger cords consisting of several funiculi. On stretching the nerve, the fibres are straightened and the striped appearance is lost. Both the peri-

neurium and endoneurium accompany the nerves in all their divisions, in some cases as far as their peripheral terminations. In the finest branches the perineurium generally becomes reduced to a single connective tissue lamella, covered on both surfaces by epithelioid cells. In this condition it is sometimes known as the sheath of Henle.

Both the cerebro-spinal and the sympathetic nerve-trunks are constructed in the manner above described, but the fibres of the cerebro-spinal nerves are chiefly of the white or medullated kind, while in nerves belonging to the sympathetic system non-medullated fibres for the most part preponderate. But very few nerves are composed exclusively of one or the other kind of fibre.

The cerebro-spinal nerve-trunks and their branches always present a brilliant whitish aspect, whereas the sympathetic nerves vary in appearance, some being whiter, others grey or reddish in colour. The more grey-looking branches or bundles consist of a large number of the pale fibres mixed with a few of the medullated kind (fig. 152) ; the whiter cords, on the other hand, contain a proportionally large amount of

Fig. 152.

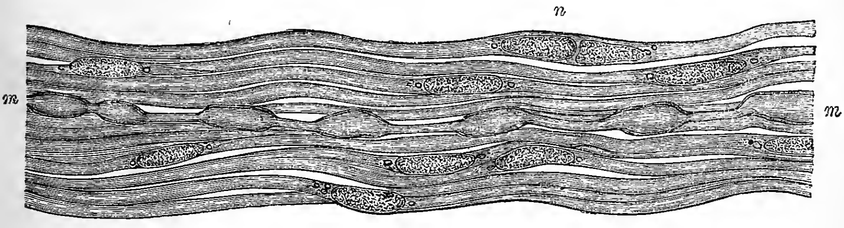


Fig. 152.—A SMALL BUNDLE OF NERVE FIBRES FROM THE SYMPATHETIC NERVE. (Key and Retzius.)

The bundle is composed of pale nerve-fibres, with the exception of the fibre *m*, *m*, which is enclosed here and there by a thin medullary sheath ; *n*, *n*, nuclei of pale fibres.

medullated fibres, and fewer of the grey ; and in some parts of the nerve grey fasciculi and white fasciculi, respectively constituted as above described, run alongside of each other in the same cords for a considerable space without mixing. This arrangement may be seen in some of the branches of communication with the spinal nerves, in the trunk or cord which connects together the principal chain of sympathetic ganglia, and in the primary branches proceeding from thence to the viscera. In the last-mentioned case the different fasciculi get more mixed as they advance, but generally it is only after the white fasciculi have passed through one or more ganglia that they become thoroughly blended with the grey ; and then, too, the nervous cords receive a large accession of grey fibres (apparently derived from the ganglia), which are mixed up with the rest, and take off more and more from their whiteness.

Differences are observed among the cerebro-spinal nerves in the proportionate amount of the two kinds of fibres which they respectively contain, and in the size of their white fibres. Volkmann and Bidder showed that whereas nerves going to voluntary muscles are chiefly

composed of large fibres, those distributed to the integuments have many small ones, and have also a larger proportion of grey fibres, moreover the anterior roots of the spinal nerves which are composed almost exclusively of motor fibres contain more large fibres in proportion than do the posterior or sensory roots. The vagus nerve contains a considerable proportion of grey fibres.

Vessels and Lymphatics.—The blood-vessels of a nerve after dividing into small branches in the epineurium and giving offsets to the groups of fat-vesicles which are there met with, pierce the layers of the perineurium obliquely, being supported by the connective tissue bundles which unite the lamellæ, and conducted into the interior of the funiculus along the septa before mentioned. Here they break up into fine capillaries which for the most part run parallel with the fibres, but are connected at intervals by short transverse branches, thus forming a network with long narrow meshes. Some of the capillaries may be observed to form loops. Lymphatic vessels are found in the epineurium, but within the funiculi there are no distinct vessels for the conveyance of lymph. It is found however that coloured fluid which is injected by means of a fine cannula into the interior of a funiculus finds its way into the lymphatics of the sheath after passing through the clefts between the lamellæ of the perineurium, so that undoubtedly a connection exists between these perineural clefts and the lymphatic system.

Course of the nerve-fibres in the nerve-trunks.—Neither in their course along the nervous cords, nor in the white part of the nerve-centres, do the medullated fibres anastomose together, nor are they observed except in rare instances to divide into branches until they approach their termination. But the nerve-trunks themselves continually ramify, and the branches of different nerves not unfrequently join with one another. The branches are of course formed by collections of nerve-fibres and it follows therefore that when two branches of nerves join, fibres pass from the one nerve-trunk to become associated with the other in their further progress, or the communication may be reciprocal, so that after the junction each nerve-trunk contains fibres derived from two originally distinct sources. In other cases the branches of a nerve, or branches derived from two or from several different nerves, are connected in a more complicated manner, and form what is termed a plexus. In plexuses—of which the one named "brachial" or "axillary," formed by the great nerves of the arm, and the "lumbar" and "sacral," formed by those of the lower limb and pelvis, are appropriate examples—the nerves or their branches join and divide again and again, interchanging and intermixing their fibres so thoroughly that, by the time a branch leaves the plexus it may contain fibres from several or even from all the nerves entering the plexus. Still, as in the more simple communications already spoken of, the fibres, so far as is known, remain individually distinct throughout.

In some instances of nervous conjunctions certain collections of fibres, after passing from one nerve to another, take a retrograde course in that second nerve, and, in place of being distributed peripherally with its branches, turn back to its root and rejoin the cerebro-spinal centre. An instance of this occurs, as shown by Volkmann, in the connection between the second and third cervical nerves of the cat, in that of the fourth cranial nerve with the first branch of the fifth, and of the cervical nerves with the spinal accessory and the descendens noni.

CONSTRUCTION OF THE GANGLIA.

Situation.—Ganglia are found in the following situations—viz.: 1. On the posterior root of each of the spinal nerves; on the corresponding root of the fifth nerve of the encephalon; and on the facial, glosso-pharyngeal and pneumogastric nerves; also on the branches of certain cerebro-spinal nerves. 2. In a series along each side of the vertebral column, connected by nervous cords, and constituting what was long considered as the trunk of the sympathetic. 3. On branches of nerves, especially of the sympathetic; occurring numerously in the abdomen, thorax, neck, and head; generally in the midst of plexuses, or at the point of union of two or more branches. Those which are found in several of the fossæ of the cranium and face are for the most part placed at the junction of fine branches of the sympathetic with branches, usually larger, of the cerebro-spinal nerves.

The ganglia differ widely from each other in figure and size: most of those which have been longest known to anatomists are conspicuous objects; but by the researches of Remak and others, it has been shown that there are numerous small or microscopic ganglia disposed along the branches of nerves distributed to the heart, the lungs, and some other viscera; and also connected with fine plexuses of nerves between the coats of the stomach and intestines.

Structure.—Ganglia are invested externally with a thin, but firm and closely adherent covering of connective tissue, continuous with the epineural and perineural sheath of the nerves: this outward covering sends processes inwards through the interior. A section carried through a ganglion in the direction of the nervous cords connected with it, discloses collections of nerve-cells, between which the nerve-fibres pass

Fig. 153.

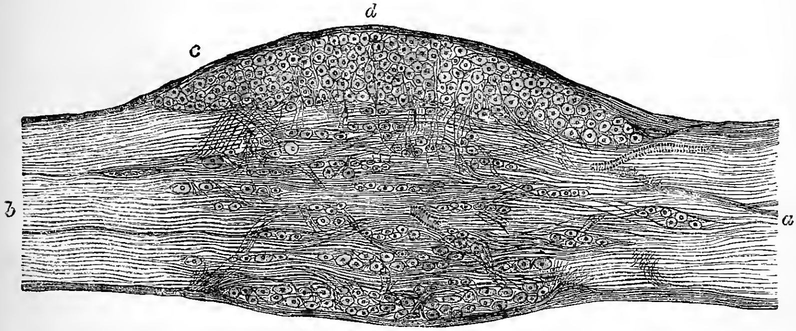


Fig. 153.—Longitudinal section through the middle of a ganglion on the posterior root of one of the sacral nerves of the dog, as seen under a low magnifying power. (E.A.S.)

a, Nerve-root entering the ganglion; *b*, fibres leaving the ganglion to join the mixed spinal nerve; *c*, connective tissue coat of the ganglion; *d*, principal group of nerve-cells, with fibres passing down from amongst the cells, probably to unite with the longitudinally coursing nerve-fibres by T-shaped junctions (see text).

(fig. 153). The nervous cords on entering lay aside the perineural sheaths, which become merged into the general connective tissue of the organ; and spread out into smaller bundles, between which the

ganglion-cells are interposed; and the fibres are gathered up again into cords, furnished with perineural sheaths, on issuing from the ganglion.

Fig. 154.

Fig. 154.—A BIPOLAR NERVE-CELL, WITH ITS POLES PROLONGED INTO MEDULLATED NERVE-FIBRES (Key and Retzius).

The whole is invested by the primitive sheath. *R*, *R*, nodes of Ranvier.

The nerve-cells have mostly a round, oval, or pyriform figure. Each cell is inclosed in a transparent capsule with nuclei upon its inner surface, (figs. 155, 156); these capsules are continuous with the primitive sheaths of the nerves (M. Schultze).

Fig. 155.

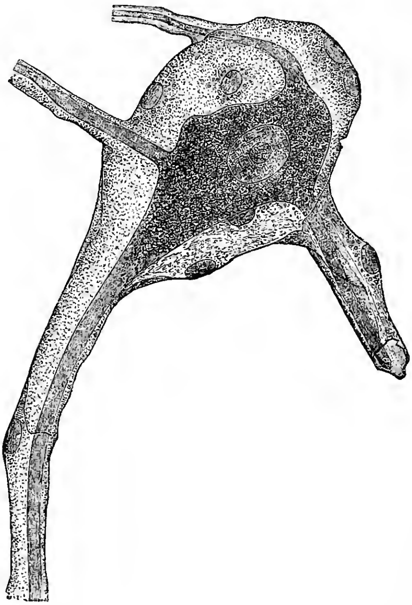


Fig. 155.—A GANGLION-CELL WITHIN ITS SHEATH; FROM THE HUMAN SYMPATHETIC. HIGHLY MAGNIFIED. (Key and Retzius.)

Of the relation between the nerve-fibres in a ganglion and the ganglion-cells, it is probable that some fibres may pass through without being connected with the cells, but that every nerve-cell is connected with a fibre or with fibres. In the case of multi-polar cells (fig. 155), such as are found in the sympathetic ganglia, each of the branches of the cell is in all probability continuous with a nerve-fibre, and the same is certainly the case with bipolar cells, at least those in which the two poles are prolonged from opposite extremities of the cell as in the spinal ganglia of fish (fig. 154), as well as

in the pyriform cells before noticed (see p. 148, and fig. 146) in which two processes arise from a part of the cell near one another, and are continued in opposite directions, either at once, or after the one fibre has made two or more spiral coils around the other or straight fibre. Uni-polar cells are found in the spinal ganglia of the higher vertebrates (fig. 156). In them the single nerve-fibre process is observed to divide before long into two fibres (*d*), which traced far enough are found to pass in opposite directions toward the ends of the ganglion. Sometimes the branches are of equal size, but they are often unequal, one being decidedly smaller than the other. As in all cases of a division of a medullated nerve-fibre, the bifurcation takes place at a node of

Fig. 156.

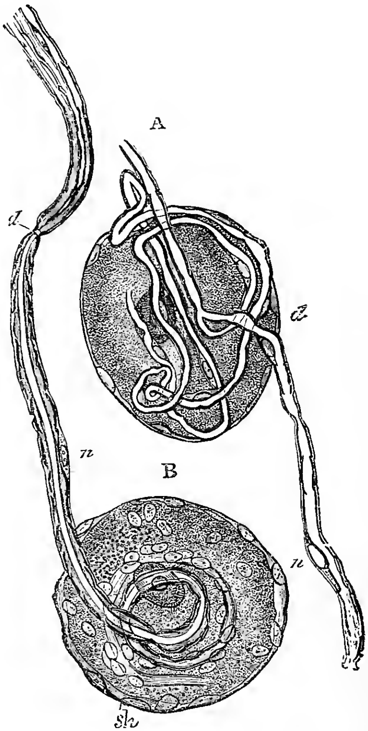


Fig. 156.—Two nerve-cells from a spinal ganglion (human) (Retzius).

sh, Nucleated sheath; *n*, *n*, nuclei of the primitive sheath of the nerve. From each cell a fibre can be seen to arise, and after a convoluted course on the surface of the nerve-cell, to bifurcate (opposite *d*); from which point the divisions pass either in the opposite direction to one another, as in A, or at first in the same direction as in B. The nuclei of the sheath of the nerve-cell are all represented in B, but only those seen in profile have been represented in A.

Ranvier, and this may be the first node from the cell, or the nerve-fibre may pass two or three or more nodes before thus dividing. The cell-process, which usually acquires its medullary sheath very soon after leaving the cell, is often convoluted over the surface of or around the cell; this is especially the case in the human spinal ganglia. Its bifurcation, or in other words its junction with a nerve-fibre traversing the ganglion is often T-shaped.

These T-shaped divisions were first noticed by Ranvier. They have been found by Retzius in the spinal ganglia of all classes of vertebrates above fishes—where the cells are bipolar like that shown in fig. 154; and also in man, in the spinal ganglia, in the jugular and cervical ganglia of the vagus, the geniculate ganglion of the facial and the Gasserian ganglion of the trigeminal; but not in the otic, the sphenopalatine, the sub-maxillary and the ciliary ganglion, the cells of all of which are multi-polar, and hence resemble those which are found in the sympathetic.

Cells which are transitional in character between the bipolar cells of most fishes and the unipolar cells with forked process of the higher vertebrates, seem

to occur, as Freud has shown, in Petromyzon, in which, in addition to the ordinary bipolar cells, some of the cells have their two processes coming off quite close to one another, and others are unipolar with a short single process which soon bifurcates to form two nerve-fibres passing in opposite directions.

ORIGINS OR ROOTS OF THE NERVES.

The cerebro-spinal nerves, as already said, are connected by one extremity to the brain or to the spinal cord, and this central extremity of a nerve is, in the language of anatomy, named its origin or root. In some cases the root is single, that is, the funiculi or fibres by which the nerve arises, are all attached at one spot or along one line or tract; in other nerves, on the contrary, they form two or more separate collections, which arise apart from each other and are connected with different parts of the nervous centre, and such nerves are accordingly said to have two or more origins or roots. In the latter case, moreover, the different roots of a nerve may differ not only in their anatomical characters and connections, but also in function, as is well exemplified in the spinal nerves, each of which arises by two roots, an anterior and a posterior—the former containing the motor fibres of the nerve, the latter the sensory.

Fig. 157.

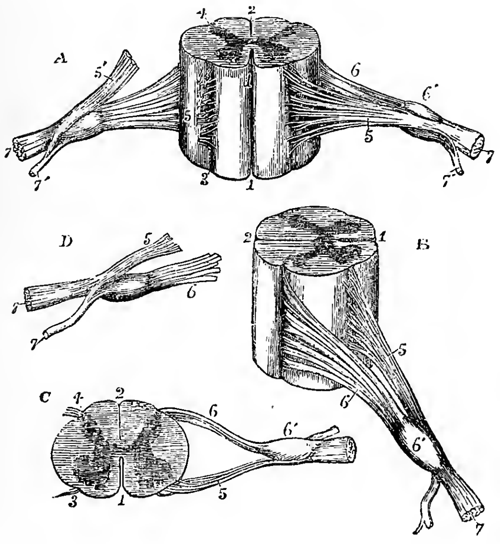


Fig. 157.—Roots of one of the spinal nerves issuing from the spinal cord. (A. T.)

A, from before; B, from the side; C, from above; D, the roots separated; 5, 5, anterior root; 6, 6, posterior root with ganglion, 6′. The full description of this figure will be found in the chapter on the cerebro-spinal nervous axis.

The fibres of a nerve may be traced to some depth in the substance of the brain or spinal cord, and hence the term "apparent or superficial origin" has been employed to denote the place where the root of a nerve is attached to the surface, in order to distinguish it from the "real or deep origin" which is beneath the surface and concealed from view.

If the deep origin be traced out, it will always be found that the nerve-fibres arise from portions of the grey substance of the nerve-centre; these portions of grey substance being sometimes known as the "nuclei of origin" of the nerve. In many cases it has been shown that the individual nerve-fibres originate as prolongations of the

nerve-cells in the grey substance (fig. 158), and where from the smallness of the cells, or the complexity of arrangement of the fibres it has not been possible to trace any such connection, it is probable that it exists none the less. It is somewhat doubtful whether the nerve-fibres originate in any other way than directly as cell-prolongations. The intermediate substance of the grey matter of the brain and spinal cord is pervaded everywhere by an exquisitely fine network of nerve-fibrils, and it has been supposed that on the one hand the ramified processes of the multi-

Fig. 158.

Fig. 158. — Ramified nerve-cell from anterior cornu of spinal cord of man (from Gerlach).

a, axis-cylinder process. *b*, clump of pigment granules. Above the cell is seen part of the network of fibrils mentioned in the text.

polar cells lose themselves in this network, and on the other hand that some of the nerve-fibres may take origin from the same general network. So that there would be in this way through the intermediate substance of the grey matter a general connection, not only of the nerve-cells, but through these and their axis-cylinder processes also of the nerve-fibres of the cerebro-spinal system.

The fibres of origin of a nerve on quitting the brain or spinal cord are in most cases collected into funiculi and acquire the connective tissue-sheaths above described. These sheaths are in continuity with the membranes investing the brain and spinal cord, and their relations will be better understood after the membranes in question have been described.

Termination, or Peripheral Distribution, of Nerves.

It may be stated, generally, and apart from what may apply to special modes of termination, that, in approaching their final distribution, the fibres, medullated and non-medullated, usually divide into branches, the division in the case of medullated fibres always occurring in the situation of a node of Ranvier (fig. 159). The axis-cylinder participates in the division; and since the white fibres frequently lose their medullary sheath shortly before they terminate, they are then represented by the

axis-cylinder and its ramifications, although the primitive sheath may continue some little way along the branches after the medullary sheath has ceased. By repeated division the fibres become smaller and smaller; but whilst some of the resulting small fibres may be simple, many are really bundles of exquisitely fine fibrils.

The fibres bear nuclei, which probably appertain to the prolongation of the primitive sheath; the nuclei are common at the bifurcations of the fibres, where they are of a triangular or irregular shape. These pale fibres often join into plexuses; but their ultimate disposition in different parts will be treated of below. As has already been explained the original dark-bordered fibres which thus undergo division and

Fig. 159.

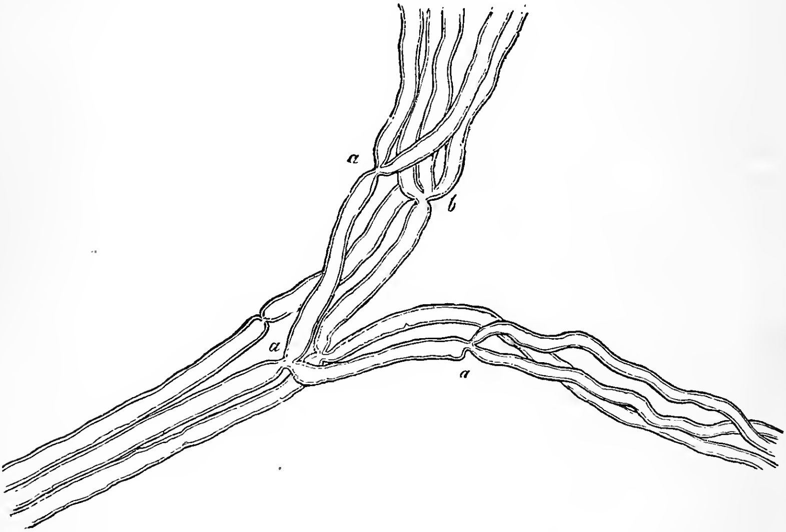


Fig. 159.—Small branch of a muscular nerve of the frog, near its termination, showing divisions of the fibres. Magnified 350 diameters (Kölliker).

a, into two; *b*, into three.

change, or which may proceed singly to end in a different and special manner, are commonly provided with a tolerably strong connective tissue sheath with nuclei, which, as it stands well apart from the dark borders of the fibre, is very conspicuous (Henle's sheath). This is derived from the perineurium which incloses the funiculi of the nerve-trunks, and, as these part into smaller collections and single fibres, undergoes a corresponding division, and finally sends sheaths along single fibres. Within the sheath of Henle fine longitudinal connective tissue fibres, with interspersed corpuscles, are seen surrounding the nerve-fibre or fibres. This tissue is a prolongation of the endoneurium.

In further treating of the termination of nerves, it will be convenient to consider the sensory and motor nerves separately.

TERMINATIONS OF SENSORY NERVES.

The sensory or afferent nerves end either in cells or in free nerve-endings, which may be simple or plexiform, and may be inclosed by cells or have an independent distribution. Of the sensory nerves which terminate in cells, the best known and longest recognised are those which are found in the organs of special sense. Here the nerves or rather their axis-cylinders, usually after dividing into fibrils, appear to end in modified epithelium-cells, which are termed *sensory* or *nerve-epithelium cells,* and are characterized for the most part by the possession of a peculiar styliform process, directed peripherally, while on the other hand they are connected centrally, as it would seem, with the nerve-fibres of the sense-organ. In the different organs of special sense these nerve-epithelium cells undergo peculiar modifications, and present certain complexities of structure which will be more properly treated of in the parts of this work which are devoted to the description of those organs.

Of the ordinary sensory nerves, including those which are devoted to the perception of tactile sensations, some end in, or in contact with, cells which are originally derived from an epithelium, but have undergone much less modification in structure than the nerve-epithelium cells above mentioned. They are termed *tactile cells* by Merkel, and he states that they may occur scattered here and there in the deeper parts of a stratified epithelium, such as the epidermis; but it is more common to find the cells in question in the true skin or other connective tissue structure, and arranged in groups of two or more, united together by a connective tissue envelope into a terminal nervous organ or *tactile end-organ.* According to most observers the axis-cylinder of the nerve ends between, not in, the tactile cells which form the chief part of the end-organ, and the cells serve rather to protect the actual nervous termination than to receive it. Of the end-organs which seem thus constructed, the best known are the *tactile corpuscles of Meissner,* the *corpuscles of Grandry,* which occur in birds, and the *round end-bulbs* of the human conjunctiva. In other end-organs (*cylindrical end-bulbs, Pacinian bodies*), the axis-cylinder passes into and seems to end abruptly in a central protoplasm-like mass, termed the core, which is surrounded by a simple or multiple expansion of the perineural sheath of the nerve, but here also, as the study of its development shows, the core was originally formed of agglomerated cells. But in many nerves of general sensation, the nerve-fibres do not terminate in a specialized organ, but the axis-cylinder becomes again and again branched, until it is resolved into filaments of extreme tenuity, its ramifications, which often unite constantly with one another and with the branches of neighbouring fibres in a plexiform manner, consisting of small bundles of ultimate fibrils, which pass at length to terminate freely, and with minute varicose enlargements, in the tissue to which they are distributed. This is the mode of ending of some of the more superficially placed nerves of the general integument, where many of the nerve-fibrils end between the cells of the stratified epithelium.

Tactile cells (Merkel). Tactile cells, isolated or in groups, but in the latter case not collected together to form a tactile end-organ, are described by Merkel as occurring in the deeper layers of the epidermis and sometimes in the subjacent true skin over almost the whole of the body. In animals they are

especially numerous in parts of the skin which are devoid of hairs, as in that which covers the soles of the feet, and on the snout, as well as amongst the epithelium-cells of the hard palate. The cells in question are round or pyriform in shape, and prolonged at one part into the axis-cylinder of a nerve-fibre: in cases where the axis-cylinder is ramified, it may be connected with more than one of these cells. Each cell is stated to be inclosed by a cell-membrane which is continuous with a prolongation of the primitive sheath of the nerve-fibres. When the tactile cells occur in the superficial layers of the cutis vera instead of amongst the cells of the epidermis they are found to be inclosed in a capsule of connective tissue, which is pierced by the axis-cylinder of the nerve-fibre as this passes to apply itself to one of the surfaces of the usually flattened cell. Such a cell, inclosed in a capsule and forming the termination of a nerve-fibre, represents, according to Merkel, the tactile end-organ in its simplest form. The existence of tactile cells such as are described by Merkel is, however, not generally admitted by histologists.

Fig. 160.

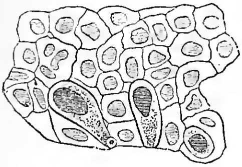


Fig. 160. — TWO TACTILE CELLS IN THE DEEPER PART OF THE HUMAN EPIDERMIS. (Merkel.)

Tactile corpuscles or touch-bodies (*Corpuscula tactûs*)—(figs. 161, 162). These were discovered by R. Wagner and Meissner in the papillæ of the skin of the hand and foot, where they are of an oval shape, nearly $\frac{1}{300}$ of an inch long and $\frac{1}{800}$ of an inch thick. One, two, or more medullated nerve-fibres run to the corpuscle and either at once or after winding round it two or more times, pass into its interior and become lost to view. The tactile corpuscles were described by their discoverers as consisting of a soft structureless core or central part, in which the nerve-fibres were thought to terminate by bulbous enlargements, and of an inclosing capsule of connective tissue, continuous with the perineurium of the nerve,

Fig. 161.

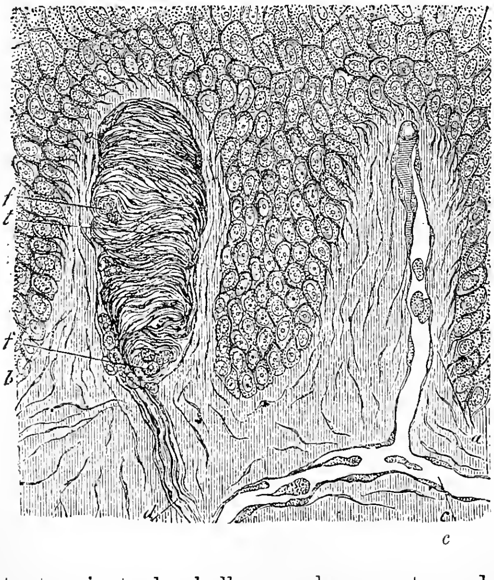


Fig. 161. — SECTION OF SKIN SHOWING TWO PAPILLÆ AND DEEPER LAYERS OF EPIDERMIS. (Biesiadecki.)

a, Vascular papilla with capillary loop passing from subjacent vessel *c*; *b*, nerve papilla with tactile corpuscle, *t*. The latter exhibits transverse fibrous markings: three nerve-fibres, *d*, are represented as passing up to it: at *f f* these are seen in optical section.

and composed for the most part of transverse or spiral fibres and nuclei, so arranged as to give the little body somewhat the aspect of a miniature fir-cone. It would appear however that a soft core, like that of the Pacinian corpuscles to be presently described, does not in reality exist in these corpuscles, but that the main substance of the touch-body is composed of connective tissue, prolonged inwards from the capsule in the form of imperfect membranous septa (fig. 163 A), between which are supported the convolutions and ramifications of the nerves, and the enlargements in which the branches of the axis-cylinder eventually end (small tactile cells according to Merkel). These terminal enlargements, which are either pyriform or globular in shape, are always placed near the capsule, and in small tactile corpuscles may occasionally project beyond it. On entering the corpuscle the nerve-fibres for the most part lose their medullary sheath, but some retain it for a short while, or it may reappear here and there in the course

Fig. 162.

Fig. 163.

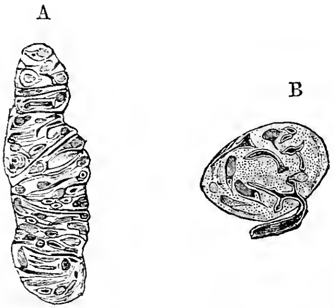


Fig. 162.—Tactile corpuscle within a papilla of the skin of the hand, stained with chloride of gold. Highly magnified. Drawn by W. Flemming, from a preparation by E. Fischer.

Ep, epidermis; only the outlines are indicated. The convolutions of the nerve-fibres within the corpuscle are well seen.

Fig. 163.—Tactile corpuscles from the palm of the hand, seen in section. (Merkel.)

A, Longitudinal section showing the interior traversed by connective tissue septa derived from the capsule; the nerve-fibres are cut across. B, transverse section at the point of entrance of a nerve-fibre, showing the axis-cylinder branching. Other nerve-fibres are cut obliquely.

of the fibres. The axis-cylinders, which are often varicose, have, as before intimated, a convoluted course before ending in their terminal enlargements.

The absence of a central core such as is found in the Pacinian corpuscles, and in some end bulbs, was first pointed out by Langerhans and afterwards by Thin. The latter observer stated as the result of his observations, that tactile corpuscles could be divided into simple or compound, according as they receive one or a greater number of nerve-fibres each nerve-fibre passing to one distinct corpuscle,

and the larger corpuscles being compounded of two or more simple ones. On the other hand, even in the same papilla, several small corpuscles may occur near to but distinct from one another.

Tactile corpuscles have been found in the following parts :—skin of the fingers, palms and soles, back of the hands and feet, volar surface of the forearm, margins of the lips, conjunctiva lining the eyelids and in the mucous membrane near the tip of the tongue.

What appear to be tactile corpuscles of simple structure were discovered by W. Krause in certain parts of the external generative organs, both in the male and female, and were named by him "genital corpuscles." Each corpuscle is composed of connective tissue, containing numerous nucleated cells, and appears not to be provided with any special capsule. The axis-cylinder of the nerve-fibre entering at one pole of the somewhat oval corpuscle (fig. 164) may either pass straight or with one or two bendings through the corpuscle, and end by a tapering (A) or by a dilated extremity (B) near the opposite pole (often projecting beyond the general body of the organ, as in B), or it may be much convoluted in its passage through the organ, so as to render it a matter of difficulty to trace its course and mode of termination. Frequently the fibre divides into two or more branches within the corpuscle, and each of these may end in a swollen extremity, which projects beyond the main part of the corpuscle; the latter then acquires a peculiar knobbed or mulberry-like aspect. The arrangement of the cells in these corpuscles seems to vary considerably. Sometimes they are chiefly collected at the exterior, leaving the part traversed by the axis-cylinder free from cells and of a fibrous appearance (fig. 164 A); but in others there is an agglomeration of cells in the centre, and the corpuscles then closely resemble the spheroidal end-bulbs of the human conjunctiva.

Fig. 164.

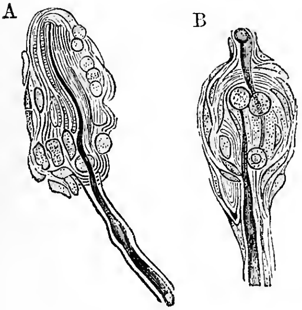


Fig. 164. — TACTILE CORPUSCLES FROM THE CLITORIS OF THE RABBIT. (Izquierdo.)

Pacinian bodies.—In dissecting the nerves of the hand and foot, certain small oval bodies like little seeds, are found attached to their branches as they pass through the subcutaneous fat on their way to the skin; and it has been ascertained that each of these bodies receives a nervous fibre which terminates within it. The objects referred to were more than a century ago described and figured by Vater, as attached to the digital nerves, but he did not examine into their structure, and his account of them seems not to have attracted much notice. In more recent times, their existence was again pointed out by Cruveilhier and other French anatomists, as well as by Pacini of Pisa, who appears to be the first writer that gave an account of the internal structure of these curious bodies, and clearly demonstrated their essential connection with nerve-fibres. The researches of Pacini were followed up by Henle and Kölliker, who named the corpuscles after him; and the Pacinian corpuscles have since been the subject of numerous

papers, to which the reader is referred for details regarding their distribution and variations, that cannot be conveniently introduced here.*

The little bodies in question are, as already said, attached in numbers to the branches of the nerves of the hand and foot (fig. 165), and here and there one or two are found on other cutaneous nerves. They have been discovered also within the abdomen on the nerves of the solar plexus, and they are nowhere more distinctly seen or more conveniently obtained for examination, than in the mesentery of the cat, between the layers of which they exist abundantly. They have been found on the pudic nerves in the penis and clitoris, bulb of the urethra, and other parts, on the intercostal nerves, sacral plexus, cutaneous nerves of the upper arm and neck, nerves of the nipple and mammary gland, and on the infraorbital nerve. Lastly they have been recognised on the periosteal nerves, and, in considerable numbers, on the nerves of the joints. They are found in individuals of all ages. The figure of these corpuscles is oval, somewhat like that of a grain of wheat,—regularly oval in the cat, but mostly curved or reniform in man, and sometimes a good deal distorted. Their mean size in the adult is from $\frac{1}{15}$th to $\frac{1}{10}$th of an inch long, and from $\frac{1}{26}$th to $\frac{1}{20}$th of an inch broad. They have a whitish, opaline aspect: in the cat's mesentery they are usually more transparent, and then a white line may be distinguished in the centre. A slender stalk or peduncle attaches the corpuscle to the branch of nerve with which it is connected.

Fig. 165.

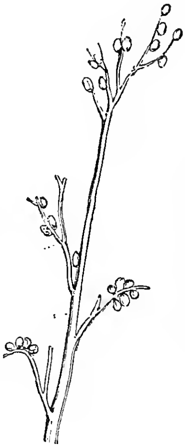


Fig. 165.—A NERVE OF THE MIDDLE FINGER, WITH PACINIAN BODIES ATTACHED. NATURAL SIZE (after Henle and Kölliker).

The peduncle contains a single medullated nerve-fibre ensheathed in perineurium, with connective tissue and one or more fine blood-vessels; it joins the corpuscle at or near one end, and conducts the nerve-fibre into it. The little body itself, examined under the microscope, is found to have a distinct lamellar structure (fig. 166, A). It consists, in fact, of numerous concentric membranous tunics encasing each other like the coats of an onion. Surrounded by these tunics, and occupying a cylindrical space in the middle of the corpuscle, is the core, formed of transparent and seemingly homogeneous soft substance, in the midst of which the prolongation of the nerve-fibre is contained. The number of tunics is various; from forty to sixty may be counted in large corpuscles. Those which are situated next to the central or median cavity, and comprehending about half of the entire number, are thinner and closer together than the more exterior ones, seeming to form a system by themselves, which gives rise to a white streak often distinguishable along the middle of the corpuscles when seen on a dark ground. Outside of all, the corpuscle has a coating of ordinary connective tissue.

The lamellæ or tunics correspond very closely in structure to the

* A complete list of papers which have appeared on this subject (and, indeed, not only on the Pacinian corpuscles, but on all the several kinds of terminal corpuscles and other sensory nerve-endings) will be found in a monograph by Prof. Fr. Merkel, "Ueber die Endigungen der sensiblen Nerven in der Haut der Wirbelthiere." Rostock, 1880.

lamellæ of the perineurium of a nerve. Each lamella (fig. 167) consists of a connective tissue layer formed both of white fibres, which have mostly a transverse direction and are placed near its surfaces (*b*), and of elastic fibres, which pass in various directions, and (with occasional bands of white fibres) stretch across the thickness of the lamella from one surface to the other (*c*). The surfaces of the lamellæ are covered

Fig. 166.

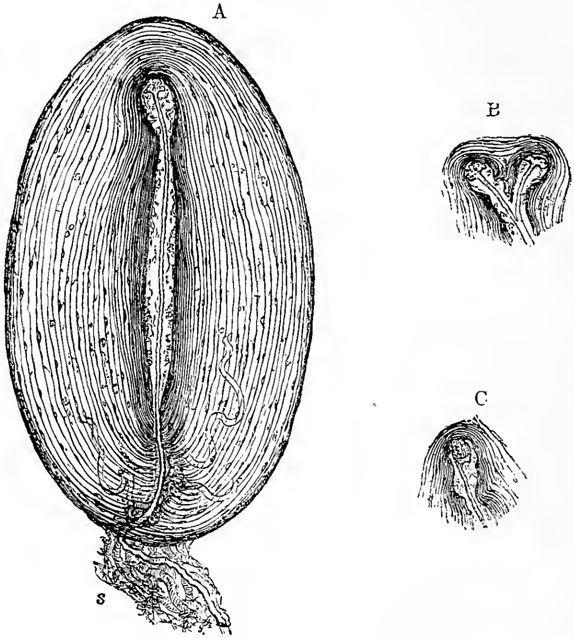


Fig. 166.—A, Magnified view of a Pacinian body from the cat's mesentery.

(From a drawing by Professor J. Marshall, F.R.S.)

s, Stalk with nerve-fibre passing to the corpuscle. One or two capillaries are also seen issuing from it between the tunics. B and C represent the termination of the nerve with the distal end of the core and adjoining tunics, and illustrate varieties of arrangement. In B the fibre is bifurcated.

with a layer of epithelioid cells (*aa*), which can be brought to view with nitrate of silver, and then their continuity with the similar cells in the perineurium is made manifest (fig. 168). The tissue of each lamella is lax as compared with that of the layers of the perineurium, and the interstices between the fibres are occupied by a considerable quantity of watery fluid, probably of the nature of lymph, and containing occasionally lymph-corpuscles. This fluid in the fresh state tends to obscure the delicate fibres of the lamellæ, so that the adjacent layers of epithelioid cells belonging to the successive lamellæ stand out sharply

when the corpuscle is viewed in optical section, and were long taken to represent the actual tunics of the organ. The epithelioid layers are not however everywhere in such close juxtaposition, but are here and there separated from one another by interlamellar spaces which are occupied by lymph, and represent the lymphatic clefts between the layers of the perineurium of a nerve.

Fig. 167.

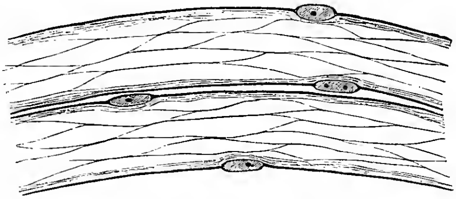


Fig. 167.—Diagrammatic representation of two tunics of a Pacinian corpuscle in transverse section.

a, a, epithelioid layers; *b, b,* connective tissue layer, more condensed near the surface; *c,* open network of fine elastic fibres in the substance of the lamella.

The nerve-fibre, the disposition of which may now be noticed, is conducted along the centre of the stalk, enters the corpuscle, and passes straight into the core, at the further end of which it terminates. As shown by Pacini, the layers of the perineurium successively become continuous with, or rather expand into the tunics of the corpuscle. Since, however, in most Pacinian corpuscles there are many more tunics in the corpuscle than layers of the perineural sheath which invests the entering nerve, it is only a few of the tunics which are thus continuous; and it will be generally found that it is the outer ones which are so. A certain number of the inner tunics are superadded therefore, and when traced towards the nerve-fibre they may be seen to end with rounded margins bounding a canal in which the nerve-fibre runs. The latter is accompanied by a little endoneural connective tissue which generally contains a number of granular cells.

Fig. 168.

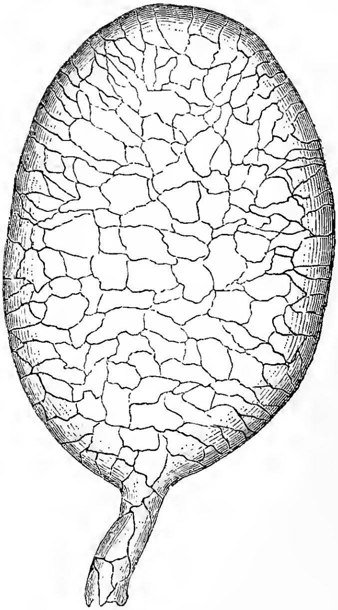


Fig. 168.—Pacinian corpuscle from the mesentery of the cat; stained with nitrate of silver. Magnified.

The epithelioid cells of the outermost tunic are shown, and their continuity, at the peduncle, with those of the corresponding layer of the perineurium (from a drawing by G. C. Henderson).

The nerve-fibre is single as it runs along the peduncle, unless when the latter supports two corpuscles; it retains the medullary sheath until it reaches the core, into which the axis-cylinder alone passes, freed from its primitive and medullary sheaths (fig. 169, *c.f.*). In its course through the core it is somewhat flattened, and presents the appearance either of a pale, finely striated, and very faintly outlined band or stripe, or of a darker and more sharply defined narrow line; differing thus in appearance according as its flat side or its edge is turned towards the eye. The contrast in the appearance of the fibre before and after entering the core is well exhibited after treatment with osmic acid, which

Fig. 169.

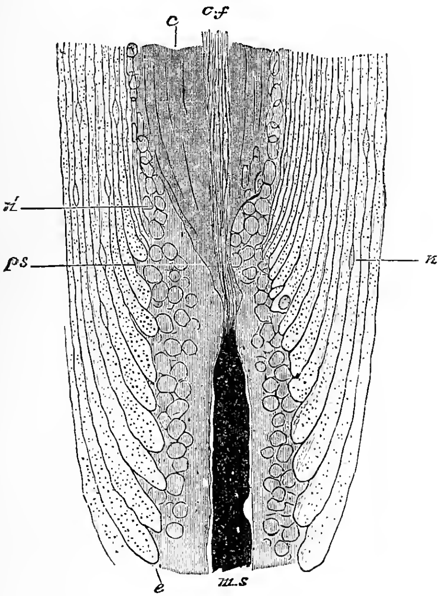


Fig. 169.—PART OF PACINIAN BODY SHOWING THE NERVE-FIBRE ENTERING THE CORE. FROM AN OSMIC ACID PREPARATION. (E. A. S.)

ms, entering nerve-fibre, the medullary sheath of which is stained darkly, and ends abruptly at the core; *p*, *s*, prolongation of primitive sheath, passing towards the outer part of the core; *c f*, axis-cylinder passing through the core as the central fibre; *e*, some of the inner tunics of the corpuscle, enlarged where they abut against the canal through which the nerve-fibre passes; *n*, nuclei of the tunics; *n'*, nuclei of the endoneurium, continued by others in the outer part of the core.

stains the medullary sheath deeply, whereas the axis-cylinder is far less stained. It sometimes happens that the fibre regains its double contour for a short space, and changes again before it terminates; this is especially liable to occur while it passes through a sharp flexure in a crooked core. The fibre usually ends by a sort of knob at the further extremity of the core, which is here itself somewhat dilated. The knob, often finely granular, appears to be an expansion of the axis-cylinder, and is sometimes of considerable size. It may be of an irregular shape with processes branching outwards from the sides, and in such cases has been taken to represent a nerve-cell; but the characteristic nucleus of the latter is absent. The ultimate destination of the processes is unknown. The axis-cylinder shows the usual longitudinal fibrillation as it passes through the core, and the fibrils become somewhat spread out as they pass into the terminal expansion. In many cases the fibre, either immediately before terminating, or in its course through the core, divides into branches: a division into three has been observed, but this is more rare. In case of division of the fibre, the core is generally, but not invariably, divided in a corresponding measure,

and the inner tunics present a figure in keeping with it. It is worthy of remark, that the nerve-fibre in its course along the core runs almost exactly in the axis of the latter, and it maintains this position even when passing through the abrupt flexures of an irregularly shaped core. It sometimes happens that a fibre passes quite through one corpuscle and terminates in a second, resuming its original size and dark outline while passing from the one to the other; and it is said that a nerve-fibre may go through two Pacinian bodies without terminating in either, returning again to the parent nerve in form of a loop (Pappenheim). A little artery enters the Pacinian bodies along with the nerve, and soon divides into capillary branches, which run up between the tunics. They then form loops, and return by a similar route into a vein corresponding to the artery: a single capillary usually accompanies the nerve as far as the core, and passes some way on the wall of the latter, sometimes with a spiral direction (Bowman). Occasionally a vessel enters the corpuscle at the distal end and passes towards the core, uniting the tunics in its passage.

As to the nature of the core of the Pacinian body, there is considerable difference of opinion. That it is not merely an expansion of the medullary sheath of the nerve-fibre, as was thought by Engelmann, is shown by its behaviour with staining fluids, and particularly osmic acid (see fig. 169). Moreover in cases where the medullary sheath is prolonged for some distance into the core, as occasionally happens, the contrast between it and the substance which surrounds it, is very marked.

In considering the true nature of the core, it should first be remarked that it is not completely homogeneous and structureless, as on superficial examination it seems to be, but exhibits at least in its outer part longitudinal striation and nuclei in variable number. In transverse section the striation in the outer part of the core is seen to be concentric, and produced apparently by flattened nucleated cells, which are so arranged as to inclose the inner and more homogeneous portion. At the entrance of the nerve-fibre into the core the nucleated cells here spoken of are to all appearance continuous with a layer of cells in the endoneurium around the entering nerve-fibre, so that this outer part of the core, at least, might be regarded as formed by an expansion of endoneurium. The inner part, on the other hand, that, namely, which is in immediate contact with the axis-cylinder, appears structureless. In its behaviour towards staining re-agents, it resembles protoplasm, and it is possible that it may represent the protoplasmic layer which in young nerves intervenes between the axis-cylinder and the sheath of Schwann of a nerve-fibre, and in which the fatty substance of the medullary sheath becomes deposited.

Some observers have described a delicate structureless sheath around the axis-cylinder here as well as in ordinary nerves.

Nothing positive is known concerning the special purpose in the animal economy which these curious appendages of the nerves are destined to fulfil. W. Krause endeavours to show that the series of concentric capsules with interposed fluid is an arrangement for converting the effect of mechanical traction into fluid pressure upon the nerve, so that tension and traction of the tissue in which the corpuscle is placed, may be felt and appreciated as ordinary pressure.

Little also is known as to their development, except that when first visible they appear in the form of small agglomerations of cells amongst which the termination of a nerve-fibre becomes lost to view.

End-bulbs.—If the conjunctiva of the calf or of certain other animals is carefully spread out and examined under the microscope, many of the

medullated nerves which course in different directions in the membrane may be seen to end in very small oval or elongated corpuscles, into the interior of which the axis-cylinder of the nerve-fibre passes, surrounded by a soft homogeneous core, to end near the extremity of the corpuscle, with a rounded or dilated termination. The core with its contained fibre is inclosed in a simple nucleated capsule composed of flattened cells. The medullary sheath ceases abruptly at the entrance of the nerve, whereas the primitive sheath appears to be continued over the core, and to line the capsule. These so-called "cylindrical end-bulbs" were discovered by W. Krause, and they have been found not

Fig. 170.

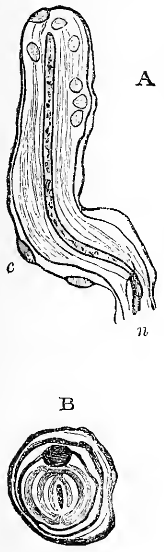


Fig. 170.—Cylindrical end-bulbs from the conjunctiva of the calf. (Merkel.)

A, in optical longitudinal section; B, in transverse section; *n*, entering nerve-fibre; *c*, nucleated capsule.

only in the conjunctiva of different animals, but in various parts of the skin and here and there in the mucous membrane of the mouth. Terminal corpuscles of this exact nature and form, have however hitherto not been observed in the conjunctiva of man nor of apes, but their place is here supplied by the small "spheroidal end-bulbs" of Krause (fig. 171, A). These (fig. 171, B, C) are composed of a connective tissue capsule (*a*) inclosing a number of polygonal cells, among which the axis-cylinder terminates. Sometimes the small medullated fibre which passes to each spheroidal end-bulb, divides into two or more branches before reaching the bulb, and the branches may be twisted around one another on their passage towards the organ (B). The capsule is continuous with the sheath of Henle of the nerve-fibre, and internally it is closely invested with a nucleated membrane, prolonged from the primitive sheath.

It will be seen that the so-called cylindrical end-bulbs closely resemble the central part or core of a Pacinian body divested of all but its innermost tunic, and, to complete the resemblance, flattened concentrically arranged cells are described by Merkel as occurring in the end-bulb as well as in the core of the Pacinian. In short, it would seem as if the little bodies in question represent the simplest of the type of terminal corpuscles of which the Pacinian corpuscles are the most complex examples; the complexity having been produced in the latter by the multiplication of the tunics. In conformity with this view it may be mentioned that Pacinian corpuscles are frequently found, especially in the lower animals, in which the tunics are few in number and the corpuscles correspondingly smaller. On the other hand, the round end-bulbs approach more nearly some of the tactile corpuscles in structure, those, namely, of a simple kind, such as are met with in birds, which form a transition to the much more complicated tactile corpuscles which occur in mammals, and especially those in the papillæ of the human hand. At the same time it cannot be supposed that there is any fundamental difference in the two kinds of end-bulb, although the arrangement of the

cells in the core and the course taken by the nerve-fibre is seemingly different, since we see that in different animals those of the one kind are replaced by those of the other kind.

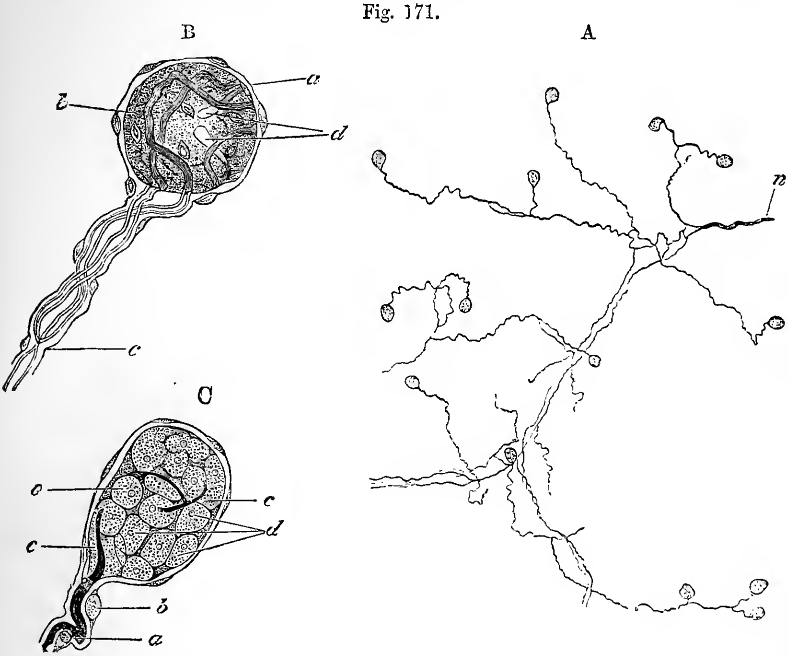


Fig. 171.—End-bulbs from the human conjunctiva. (Longworth.)

A, Ramification of nerve-fibres in the mucous membrane, and their termination in end-bulbs, as seen with a lens; B, an end-bulb more highly magnified; *a*, nucleated capsule; *b*, core, the outlines of its component cells are not seen; *c*, entering fibre branching and its two divisions passing to terminate in the core at *d*; C, an end-bulb treated with osmic acid, showing the cells of the core better than B; *a*, the entering nerve-fibre; *b*, capsule with nuclei; *c*, *c*, portions of the nerve-fibre within the end-bulb, the ending of the fibre is not seen; *d*, *e*, cells of the core.

On account of the light which they throw upon the structure of the end-organs of mammals, a short description of the tactile end-organs of birds may not be out of place here.

Tactile corpuscles of birds.—It was noticed by Grandry that in the soft skin covering the bill of certain birds, such as the duck and goose, a peculiar form of end-organ exists consisting of two or more flattened cells, enclosed in a common capsule of connective tissue, and receiving between them the termination of the axis-cylinder (fig. 172). The structures in question have since been investigated by Merkel, Key and Retzius, Ranvier and Hesse, and more recently by Izquierdo, with the following results :—

The cells which form the corpuscle of Grandry are for the most part of no great thickness, and the surfaces which are opposed to one another are flattened. Their protoplasm is stated by Merkel to resemble that of nerve-cells, having a striated aspect, the striæ being partly concentric with the periphery of the cell, partly passing radially through it. The nucleus has also been compared to that of a ganglion-cell. There may be two only of these cells (which are termed by Merkel "tactile cells," by others "protective or inclosing cells") in a corpuscle of Grandry, or there may be three or four or even more, piled the one on the other. When numerous they may lose their regularity of arrangement. Occupy-

ing the interval between every two cells is a flattened disk termed the "tactile disk," and according to the testimony of all the above-named observers the axis-cylinder of the entering nerve-fibre ends in these tactile disks. According to Merkel, the disk is itself, on the other hand, directly in continuity with one or both of the cells between which it lies. The tactile cells and disks are all inclosed in a common capsule or sheath of connective tissue continuous with the perineurium of the nerve and receiving also a lining from the nucleated sheath of Schwann. From the capsule incomplete septa pass inwards between the flattened cells, as far as the edges of the tactile disks, so that the septa look as if they were perforated to receive the disks. Usually a single nerve-fibre passes to each corpuscle, and this may either lose its medullary sheath on entering the corpuscle or may retain it for some part of its course, although it eventually, in any case, becomes lost. The axis-cylinder, passing between the capsule and the tactile cells, divides into as many branches as there are tactile disks, in which, as already mentioned, it finally terminates.

It will appear from the above account that the chief point in which there is a difference of opinion with regard to the structure of these simply constructed tactile corpuscles, is as to the expansion of the axis-cylinder known as the tactile disk, whether this is prolonged or not into the cells which cover it. The former view is taken, as we have seen, by Merkel, but the opinions of most other observers are adverse to it. There is, however, this to be said in favour of Merkel's view, namely, that when degeneration takes place as a result of the section of the nerve, the degenerative process extends not only to the tactile disk but also to the cells which cover it.

These corpuscles are developed as a result of the multiplication and downgrowth of some of the epithelium-cells which lie at the apex of a papilla (fig. 172, C). The growth becomes entirely cut off from the rest of the epithelium and surrounded by connective tissue, whilst the cells in it are converted into the flattened "tactile cells," and a prolongation of a nerve-fibre grows up into it.

Fig. 172.

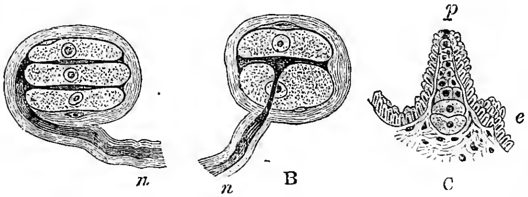


Fig. 172.—Tactile corpuscles from the duck's tongue. (Izquierdo.)

A, composed of three cells, with two interposed disks, into which the axis-cylinder of the nerve, *n*, is observed to pass; in B there is but one tactile disk enclosed between two tactile cells; C illustrates the development of a tactile corpuscle like the one shown in B; *e*, deeper cells of the epithelium covering the papillated surface of the tongue; *p*, apex of a papilla, in which there is seen to be a downgrowth of epithelium-cells, the lowermost of which are developed into tactile cells.

Other modes of ending of sensory nerves. Instead of ending in the special terminal corpuscles of different kinds which have been described in the preceding pages, many sensory nerves, as before stated, terminate in the form of fine ramifications of the axis-cylinder, which pass between the elements of the tissue to which the nerves are distributed, and may either simply come in contact with them, or, it is believed, may in some cases form an actual connection with the cells. As they approach their termination the sensory nerve-fibres, which are generally medullated, divide

dichotomously again and again, retaining after all the earlier divisions both the medullary sheath and the primitive sheath, and being accompanied by a prolongation of the sheath of Henle. Lower down this last-named sheath becomes lost, and a short distance further on the medullary sheath also disappears, the nerves being continued as pale fibres inclosed only by the nucleated sheath of Schwann. Within this it can distinctly

Fig. 173.

Fig. 173.—Distribution of nerves in a portion of the cornea of a frog. (Klein.)

The nerves are stained with chloride of gold. *a*, *a*, part of a plexus of non-medullated fibres, made up of numerous fine fibrils; *b*, *b*, smaller fibres derived from them, and themselves giving off still smaller branches, *c*, *c*, which are composed of single fibrils.

be seen in preparations stained with chloride of gold, that the axis-cylinder is made up of fine varicose fibrils (fig. 173, *a*, *a*). At every division of the nerve some of these fibrils pass into each branch, and where, as often happens, the branches unite with one another so as to form a subterminal plexus, some of the fibrils pass across from one branch to another. By the time the terminal ramification is reached many of the branches may consist of only one or two ultimate fibrils (*c*, *c*). It is generally found that the sheath of Schwann has ceased long before this condition is arrived at, although nuclei apparently like those of that sheath may often be still seen here and there upon the branches, especially at the points of bifurcation. Finally, the branches of the nerve, thus reduced to the condition of ultimate fibrils, often varicose, pass between the tissue elements, and may there form an actual network by joining one with another and becoming fused together at the points of junction, or may

end either simply or with small knobbed extremities without uniting with other fibrils into a nervous network; or, according to the view of some histologists, may pass into the cells of the tissue and thus terminate.

A "nervous network" is not to be confounded with a "nervous plexus." In the former an actual fusion of the ultimate fibrillæ which result from the division of the axis-cylinders of the nerves is assumed to take place, whereas in the latter, although there may appear to be an intimate union between the different nerves which enter into the plexus, this union does not extend to the ultimate elements of the nerve-fibre; in other words, although fibres or parts of fibres (fibrils) may be given and received by the several nerves to and from one another, these fibres (in the case of the larger plexuses) or fibrils (in the microscopic plexuses) remain completely distinct, although they may run in close juxtaposition. Nervous plexuses are of very common occurrence, both those of the larger sort which have long been recognized by anatomists, and the smaller microscopic plexuses which are very often found near the endings, both of some centripetally conducting, and of some centrifugally conducting nerves. But nervous networks are far less frequent than has been supposed, although they were until lately described as a mode of nerve-termination not by any means rare, and indeed their existence is now doubted altogether by some histologists. (Compare *Waldeyer*, Ue. d. Endigungsweise der sensiblen Nerven: Archiv f. mikr. Anat. XVII. s. 367.)

Nerve-endings in tendon.—Special modes of ending of sensory nerves have been described in various peripheral organs, but those only which are found in the tendons of muscles will here be noticed, the modes of termination in other parts being deferred until the several organs are treated of.

Most of the nerve-endings in tendon seem referable to one or other of the end-organs which have just been described, although they present considerable modification of form. Thus in many tendons, at their junction with the muscles, there occur, according to Golgi, long spindle-shaped bodies, composed apparently of a modified connective tissue, into which one or more medullated fibres pass, and after dividing once or twice diverge towards the periphery of the corpuscle, where they end as pale fibres in small granular swellings. In other tendons end-bulbs like those in the conjunctiva are found (Sachs), and small Pacinian corpuscles of simple structure occur occasionally in the areolar tissue sheaths of tendons and ligaments. Rollett describes the non-medullated nerves which pass to the tendon of the sterno-radial muscle in the frog as ending in peculiar flattened end-organs comparable to the end-plates of muscle presently to be described.

Lastly, some observers have described the nerves of tendons as ending, in part at least, in the form of ramifying pencils of pale fibres, usually varicose, and terminating freely, by fine tapering extremities, between the tendon bundles. This is similar to the way in which the nerves appear to end in the substantia propria of the cornea, which is also a form of fibrous tissue and receives a large number of nerve-fibres. But a detailed description of the manner in which the nerves of the cornea are distributed will be more conveniently deferred until the eye is treated of.

TERMINATIONS OF MOTOR NERVES.

In the **involuntary muscles** such as those which constitute the muscular layers of the hollow viscera, the nerves, which are for the most part non-medullated with a small intermixture of white fibres, form complicated plexuses as they near their termination. At the junctions of the fine nervous cords which compose the plexuses groups of ganglion-cells are in many parts met with; a well known example of such a gangliated plexus being the *plexus myentericus* of Auerbach between the longitudinal and circular layers of the muscular coat of the intestine. From these gangliated plexuses branches are sent off, which penetrate between the elements

of the involuntary muscular tissue, coursing for the most part parallel with the muscular fibres. The pale nerve-fibres bifurcate and give off branches at acute angles at frequent intervals, and eventually become separated into fine filaments which may represent ultimate fibrillæ, but the branches which are given off only rarely, according to Löwit, become united with those from adjoining nerve-fibres, so that it can scarcely be said that an intramuscular plexus, and still less a network, really exists. The fine longitudinally coursing fibrils come into close relation with the involuntary muscle-cells, but do not appear to pass into the interior of the cells and their nuclei, as was stated by J. Arnold. They are said to end by gradually tapering or varicose extremities, but according to Elischer each nerve-fibril terminates by a slight bulbous expansion opposite the nucleus of a contractile cell.

In the **cardiac muscular tissue** the nerves form networks with very long meshes. The nervous fibrils become closely applied to the muscular fibres but do not penetrate the latter according to Fischer, nor are motorial end-plates, such as occur in voluntary cross-striated muscle, to be found in the heart. L. Gerlach, on the other hand, affirms the penetration of the muscular cells by nerve-fibrils.

The **nerves of voluntary muscles** terminate for the most part in special expansions, to which the term *motorial end-plates* has been applied.

As mentioned in the account of the muscular tissue, the nerves in the voluntary muscles form plexuses, of which the branches grow finer and the meshes closer as they advance further into the tissue. The

Fig. 174.

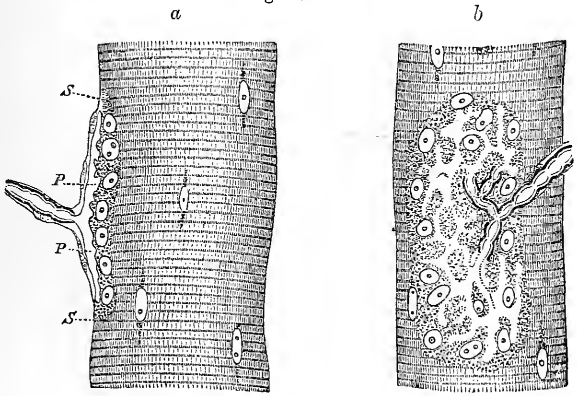


Fig. 174.—Nerve-ending in muscular fibre of a lizard (Lacerta viridis), according to Kühne. (Highly magnified.)

a, end-plate seen edgeways; *b*, from the surface. *s*, *s*, sarcolemma; *p*, *p*, expansion of axis-cylinder. In *b* the expansion of the axis-cylinder appears as a clear network branching from the divisions of the medullated fibre.

individual fibres, while still associated in small bundles, undergo division (fig. 159), and at length single dark-bordered fibres pass off to the muscular fibres. These nerve-fibres on approaching or reaching a muscular fibre often divide still further. The branches retain their medullary sheath until they reach the sarcolemma, when the white substance abruptly terminates, while the primitive sheath becomes continuous with

the sarcolemma (Kühne, fig. 174, *s*). Ranvier states, however, that it is a prolongation of the nucleated sheath of Henle, and not the primitive sheath which is continuous with the sarcolemma. The axis-cylinder as it passes into the fibre forms a clear localised branched expansion (*p p*), which lies immediately under the sarcolemma, embedded in a layer of granular matter which contains a number of large clear nuclei, each having one or more bright nucleoli. The termination of the axis-

Fig. 175.

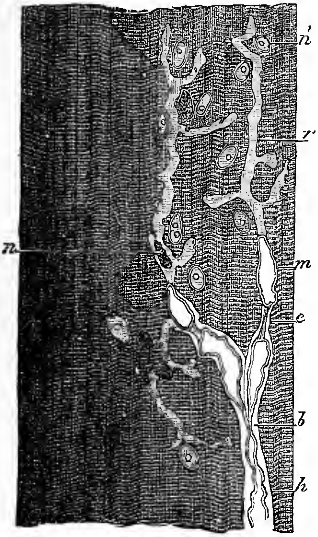


Fig. 175.—Termination of a nerve in a muscular fibre of the lizard (Lacerta viridis). (Ranvier.). Very highly magnified.

h, outer sheath of the nerve-fibre (sheath of Henle, according to Ranvier); *b*, bifurcation of the fibre; *e*, node; *m*, short segment beyond the node; *r*, terminal ramifications of the axis-cylinder; *n*, nuclei on the branches of the axis-cylinder; *n'*, nuclei in the granular substance of the end-plate. The granular substance lies in the intervals between the branches of the axis-cylinder; it is not seen in this figure.

cylinder is not in the form of a continuous plate, as was thought by Rouget, but appears when viewed from the surface in the form of an arborescent figure (fig. 175), the branches of which do not, according to Ranvier, anastomose. Attached to these branches small granular nuclei (*n*) are seen at intervals; these are not to be confounded with the clear nuclei of the granular substance (*n'*), nor with certain flattened nuclei which lie immediately under the sarcolemma covering the end-plate, and which resemble the nuclei of the nerve-sheath. The sarcolemma over the situation of the nerve-ending is slightly raised above the general surface (fig. 174 *a*). It would appear that a muscular fibre, when short, has but one terminal structure, and receives consequently but one nerve-fibre. As, moreover, the fibres of a nerve undergo division, probably repeated division, before ending, it follows that one fibre in a nerve-root or -trunk may supply several muscular fibres. Longer muscular fibres have two or more nerve-endings.

In amphibia (fig. 176) there is no granular substance with clear nuclei imbedded in it, and the ramifications of the axis-cylinder are extended over a larger proportionate area of the fibre than in scaly reptiles, birds, and mammals, so that the termination of the nerve is less localised. The branches of the axis-cylinder run for a short distance parallel with the axis of the fibre between the sarcolemma and muscular substance, terminating abruptly by rounded extremities. They present here and there slight enlargements, connected with which are seen, as in the end-plate of the lizard, granular pear-shaped nuclei (*b*), entirely different in appearance from the proper nuclei of the muscle (*e*). A fine tortuous fibril is stated by Kühne to be given off from the pale fibre to each of these granular nuclei, and to terminate in it by a bulbous enlargement.

It would appear then that in all classes of vertebrates the nerve-fibres

which are distributed to the voluntary muscles, terminate in the form of a ramification of the axis-cylinder on the surface of the fibre within the sarcolemma, but that in some the branches cover a far greater extent of the surface of the fibre than in others.

The termination of motor nerves in special granular expansions within the sarcolemma was first noticed by Doyère in insect-muscle. The arborescent termination of the axis-cylinder was discovered in the frog by Kühne in 1862. In the same year the end-plates were recognised by Rouget in the lizard, and in 1863 by W. Krause in mammals. The last named observer was the first to describe the termination of the axis-cylinder as a ramified expansion imbedded in granular substance, but maintained that the whole structure lay outside the sarcolemma. The above account may, however, be taken as the one most in accordance with the more recent researches on the subject, and as probably on the whole correct. It should be stated at the same time that the existence of localised end-plates has been called in question by Gerlach, who from the study of muscular fibres prepared with chloride of gold and potassium arrived at the conclusion that the axis-cylinder of the nerve after passing through the sarcolemma forms a close network of minute varicose fibrils throughout the muscular substance, with which they are closely incorporated. Moreover, another observer, Arndt, who, it is true, admits the existence of the end-plate, describes in addition, a complex system of communicating fibres which extend throughout the muscular substance, and is the means of bringing the plate into connection with the muscle corpuscles and nuclei. These statements, however, have not hitherto received confirmation, although Engelmann and Fœttinger have been led from observations upon insect-muscles to form a conclusion which is at least somewhat analogous, to the effect, namely, that the expansion of the nerve-fibres comes into actual continuity with the isotropous substance of the muscular fibre. But the effect of section of a motor nerve in the living mammal—the resulting degeneration extending no further into the muscular fibre than the end-plate itself—is a strong argument against the existence of any such anatomical continuity.

Fig. 176.

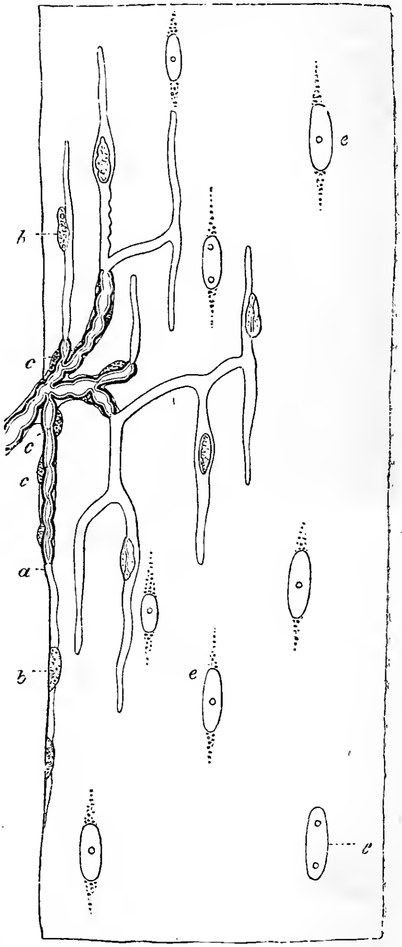


Fig. 176.—Nerve-ending in muscle of frog (Kühne).

a, one of the branches of the medullated fibres passing within the sarcolemma; *b*, *b*, granular pear-shaped nuclei; *c*, *c*, nuclei of sheath; *e*, *e*, muscle-nuclei.

DEVELOPMENT OF NERVES.

It has been shown by Balfour in elasmobranch fishes, and by Milnes Marshall in the chick, and the same is probably the case in mammals, that the nerve-roots and their ganglia, and in all probability the nerves generally, develope as cell-outgrowths from the rudimentary central nervous system. The latter, as has long been known, is formed by an involution of the ectoderm or epiblast along the middle line of the embryo. So that not only the nerve-cells and -fibres of the central nervous system (brain and spinal cord), but also the peripheral nerves, and the nerve-cells of the ganglia in connection with them, are of ectodermal origin. No doubt the connective tissue which enters into the construction of the nerves and nerve-centres, as well as the blood-vessels which are distributed in them, are mesodermal, having become formed as ingrowths from the surrounding mesoderm, but it is as yet uncertain whether this statement holds good with regard to the substance (*neuroglia* of Virchow, *reticulum* of Kölliker) which occupies the interstices between the proper nervous elements within the nerve-centres. For according to Kühne and Ewald this substance exhibits so marked a resistance to the action of tryptic digestive fluids as to be comparable only to horny substance, and it is accordingly termed by them neuro-keratin. And since horny matter is not found except in connection with epithelial tissues, it is inferred by them that the neuro-keratin must be developed from some of the ectoderm-cells rather than from the included mesoderm. However this may be, it seems at least to be definitely ascertained that the nerve-cells in the nervous centres are derived from the ectoderm-cells, which, undergoing enlargement and modification, both in their substance and form, send out branches at one or more points of their surface, and acquire the specific characters of nerve-cells.

But with reference to the formation of the nerve-fibres, both within the nervous centres and in the peripheral nerves, the knowledge as yet acquired is not very positive or consistent. It appears, however, to be certain that their development in both situations proceeds distalwards, and that the medullated fibres are originally formed as pale fibres, and only later acquire their medullary sheath. This change occurs, not simultaneously over the whole nervous system, but in regular order along definite tracts, and the knowledge of this, in the hands of Flechsig, has proved an important means of tracing the course of certain strands of fibres in the nervous centres, as will be noticed when the subject of the continuity of the fibres in those centres is dealt with.

According to the view which has generally been taken, nerve-fibres are formed by the linear coalescence of elongated cells, in the peripheral parts of whose protoplasm the fatty matter of the medullary sheath gradually accumulates, at first in the form of fine granules, and thus transforms the originally pale fibres into dark bordered fibres. This change of aspect is apparent in many nerves of the human embryo of the fourth or fifth month. According to Kölliker's account, the nerve-fibres in the tadpole's tail are prolonged by lines of fusiform cells, which coalesce into pale fibres. These send out fine offshoots, which may join with neighbouring fibres, or with branched cells, which become fibres, and in both of these ways the growth and branching of the nerves go on. The first fibres thus generated (embryonic fibres) virtually represent bundles of two, three, or more permanent fibres, into which they are speedily converted by cleavage; while the formation of the medullary sheath proceeds outwards along the branches.

But if, as seems to be the case, when a nerve has been cut and has undergone degeneration, the axis-cylinders are reproduced along the whole length of the distal part by a downgrowth from the axis-cylinders of the central cut end, it is probable that a similar mode of formation of the nerves may occur originally, and that the axis-cylinder is to be regarded as a continuous outgrowth from one of the nerve-cells of the nervous centre. With the medullary sheath, however, the case may be different. For this, as we have seen, is divided at regular intervals into a series of internodes, each of which possesses a nucleus, and may therefore, as Ranvier pointed out, be looked upon as representing a cell, the primitive sheath being homologous to the cell-membrane. It is not improbable, therefore, that each such internode is actually formed from an elongated

cell, developed around a previously formed axial fibre, and filled with the fatty matter of the medullary sheath in the same way as the connective tissue-cells become filled with fat in the development of the adipose tissue. In support of this view it may be noted that in young nerves the segments are shorter than in the adult, and there is a layer of homogeneous or finely granular protoplasmic substance outside the medullary sheath, between it and the primitive sheath: as the nerves increase in size this layer, being more and more encroached upon by fatty substance, eventually disappears, except in the immediate neighbourhood of the nuclei. In the brain and spinal cord at an early period of development flattened cells are said by Ranvier to be applied to the medullated fibres, but they subsequently disappear or become incorporated with the interstitial tissue of those organs.

The fact that the nerve-segments of the peripheral nerves are considerably shorter in the young animal, points to the existence of an interstitial as well as a terminal growth of nerve-fibres.

Degeneration and regeneration of nerves.—The divided ends of a nerve that has been cut across readily reunite by cicatricial tissue, but the cut ends of the fibres themselves do not thus unite. On the contrary, soon after the section, a process of degeneration begins in the peripheral or severed portion of the nerve. The nuclei become multiplied, and the protoplasm about them largely increased in amount, the segments taking on to some extent their embryonic condition. At the same time the medulla of the white fibres degenerates into a granular mass consisting of fatty molecules, and is then totally removed, and eventually the axial fibre also disappears (fig. 177, A, B, & C).

In regeneration the new fibres grow afresh from the axial fibres of the central end of the divided nerve-trunk (often more than one from each); and, penetrating into the peripheral end of the trunk, grow along this as the axis-cylinders of the new nerves, becoming after a time surrounded with medullary substance (fig. 177, D).

To this brief summary the following details may be added:—In warm-blooded animals the first changes in the peripheral part of the nerve are seen twenty-four hours after the section. The nuclei underneath the primitive sheath are everywhere found hypertrophied, the primitive sheath is distinctly visible, and protoplasm is found to have accumulated at the expense of the medullary sheath, both in the immediate neighbourhood of the nuclei, at the nodes, and also at other points in the fibre, which correspond, according to Ranvier, with the intervals between the medullary segments. Fifty hours after the section in the rabbit (but not till four days in the dog) the protoplasmic aggregations are found here and there altogether to interrupt the continuity of the medullary sheath, and they contain numerous fatty granules, and sometimes droplets of myelin (fig. 177, A). About the fourth day the nuclei are seen to be multiplied, but not to any great extent (C); and the whole of the myelin after four or five days is broken up into drops, some larger, some smaller. The axis-cylinder is also found to be interrupted at numerous places, and remains only in the shape of short fibres, often curled round at their broken ends, enclosed in the large drops of myelin (B). Eventually these portions also may disappear. The myelin at length becomes almost entirely removed, until nothing remains of it except a few isolated drops, which escape absorption, and all that then remains of the original fibre is the primitive sheath, which is occupied by a protoplasmic mass containing an increased number of nuclei. During the disappearance of the myelin from the nerve-fibres the cells of the connective tissue in the neighbourhood of the fibres become charged with fatty granules, which may have become formed from the dissolved fatty substances of the medullary sheath.

These degenerative changes seem to occur simultaneously along the whole length of the nerve. In the nerves to voluntary muscles the end-plate is said, however, to be the part first affected.

In the immediate neighbourhood of the section the appearances are somewhat modified by the escape of the myelin from the cut ends of the nerve-fibre, and the infiltration of blood and lymph into the interior of the ends thus emptied of their contents. This change must of course occur both in the central stump of the nerve as well as in the peripheral cut end: it does not often extend beyond the

first node. Apart from such traumatic modification, true degenerative changes do not according to Ranvier occur in the end of the nerve which is still in connection with the centre, although proliferation of the nucleus in the first and second inter-

Fig. 177.

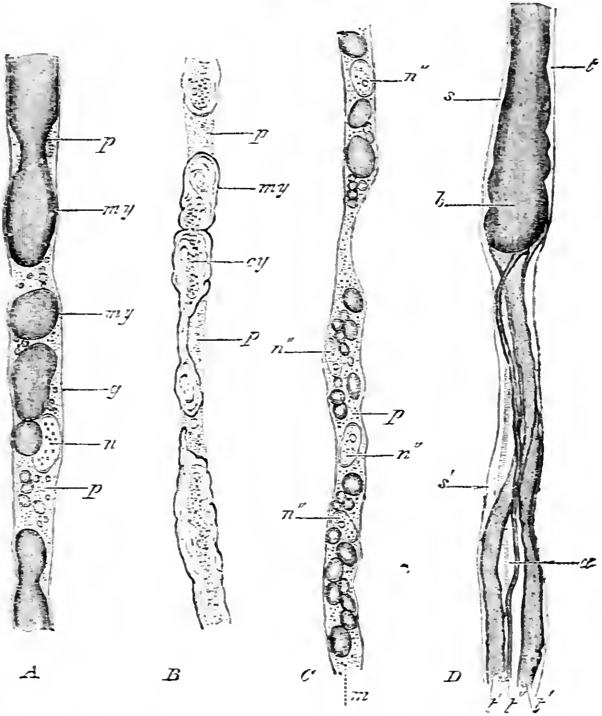


Fig. 177.—Degeneration and regeneration of nerve-fibres in the rabbit (Ranvier).

A, Part of a nerve-fibre in which degeneration is commencing in consequence of section (50 hours previously) of the trunk of the nerve higher up; *my*, medullary sheath becoming broken up into drops of myelin; *p*, granular protoplasmic substance which is replacing the myelin; *n*, nucleus, not yet multiplied; *g*, primitive sheath. B, another nerve-fibre in which degeneration is proceeding, the nerve having been cut four days previously. This specimen is differently prepared from the others, so as to exhibit the axis-cylinder (*cy*) also partly broken up into portions of different length, enclosed in the myelin, *my*. C, more advanced stage of degeneration, the medullary sheath having in great measure disappeared, while several nuclei (*n″*, *n″*) have been formed by division of the single nucleus of the internode. D, commencing regeneration of a nerve-fibre. Several small nerve-fibres (*t′*, *t″*) have sprouted out from the enlarged cut end (*b*) of the nerve-fibre (*t*); *a*, an axis-cylinder, which has not yet acquired a medullary sheath; *s*, *s′*, primitive sheath.

nodes near the cut may take place. The central cut end of the axis-cylinder does not become altered; except that it undergoes a slight swelling, preparatory in all probability to the renewed growth by which the regeneration of the fibre is effected.

Regeneration proceeds but slowly. Up to the twenty-eighth day after the section, or even later than this, there is still no trace of new nerve-fibres in the peripheral part of the nerve. With the exception of a few fibres which for some reason not well understood (probably because they are derived from some other nerve which has not been cut, and are merely taking a recurrent course in the cut nerve), have not undergone degeneration, nothing is to be seen in a section of the nerve at this period, except the primitive sheaths of the old fibres, filled

with clear or finely granular substance. If, however, a transverse section be made of a nerve considerably later than this (sixty or seventy days after the original section) it is found that within the tubes formed by the old primitive sheaths, and also in some places between them, small single fibres or groups of fibres, either pale or provided with a medullary sheath, are to be seen, besides here and there those drops of myelin which have remained unabsorbed from the medullary sheaths of the original fibres. On cutting out the central end of the nerve, together with the cicatrix, and separating its fibres, it is seen that the groups of small fibres noticed in the transverse section are continuous with the central ends of the axis-cylinders of the original nerve (fig. 177, D). Either a bunch of small fibres may grow directly from the axis-cylinder of one fibre, or two only may emerge from this; but these soon bifurcate, and, repeating this process again and again, may eventually form a considerable group. It would appear therefore that the regeneration of a cut nerve is effected by a growth of new fibres from the axis-cylinders of the central cut end, and that many more such fibres are formed in the first instance than the old ones which have undergone degeneration. The growth from the old axis-cylinders always occurs in the situation of a node—either the one nearest to the section or one somewhat higher up. The new fibres are at first pale but subsequently acquire a medullary sheath, with constrictions of Ranvier, which, as in young nerves, are placed at much more frequent intervals than in the old fibres, so that the intervals are much shorter.

The groups of fibres which grow thus in groups from the old axis-cylinders are often very irregular in their course, twisting around one another, and even looping back in some places for a considerable distance. In the cicatrix especially is this irregularity and obliquity of disposition noticeable, probably on account of the absence here of the guide formed by the sheaths of the original fibres.

Restoration of function in the nerve does not occur for several months, during which time it may be presumed the new nerve-fibres are slowly finding their way along the course of those which have been destroyed as a result of the section. Of the numerous fibres in the groups above described, no doubt a few only eventually assume the function of the fibres which they replace, but the later steps of the process of regeneration have not yet been fully followed out.

Except at the actual place of section the connective-tissue sheaths of the nerves remain unaltered. In the cicatrix the new nerve-fibres do not at first run in definite sheaths, but these become subsequently developed from the connective-tissue around, so that at length the restoration of continuity of all the structures in the nerve becomes complete.

Ranvier looks upon the regeneration of a nerve by growth from the intact central ends of the fibres as illustrating the tendency which, he believes, all nerve fibres exhibit, to grow continuously until a hindrance is met with, and he compares the result of cutting a nerve-fibre in causing the growth of a number of new fibres in place of the original one, to that produced when the leading shoot of a plant is removed, in causing the production of a number of lateral buds.

Some have thought that under favourable circumstances an immediate union between the ends of the nerve-fibres may happen after section; but considering the impossibility of procuring exact apposition of the individual fibres, end to end, as well as the inevitable extension of the effects of the mechanical injury caused by the section along the soft contents of the primitive sheath, it seems improbable that such direct union should occur.

The degeneration does not affect, as we have seen, the part of the nerve remaining in connection with the nervous centre, which seems to exert an influence in maintaining the nutrition of the nerve. The ganglia, as well as the grey matter of the brain and spinal cord, are centres of this influence. It is found that, in the central portion of a divided spinal nerve, while the fibres belonging to the anterior root owe their integrity to their connection with the spinal cord (and especially with the large cells of the anterior cornu), those of the posterior root are similarly dependent on the ganglion: and that, if the posterior root be cut between the ganglion and the spinal cord, not only will the fibres which pass from it into the trunk of the nerve beyond the ganglion remain unchanged, but also those above the ganglion in the portion of the root left in connection with it; whereas the fibres of the same root which remain connected with the cord but severed

from the ganglion degenerate. Section of the sympathetic nerve in the neck is followed by degeneration of the upper segment as high as the superior cervical ganglion, but no further.

The degeneration of the peripheral end of a cut nerve and the breaking up of the substance of the medullary sheath were first noticed by Nasse in 1839. But the discovery by Augustus Waller in 1852 of the dependence of the process upon isolation of the nerve-fibre from its nutritive centre, and his application of this discovery to the tracing the course of nerve-fibres in peripheral parts (now known as the Wallerian method) first gave full interest and importance to the observation of Nasse. The result has been the appearance of numerous writings upon the subject, the latest being those of Ranvier, whose account has been closely followed in the text.*

Recent Literature of the Nervous Tissues.—On the Structure of Nerves, &c.—*Frommann*, in Virch. Arch. 1864 & 1865 ; *Beale*, in Arch. of Medicine, 1865 ; *Deiters*, Ue. Gehirn u. Ruckenmark, 1865; *Courvoisier*, in Arch. f. mikr. Anat. II., 1866 ; *Kollmann u. Arnstein*, in Zeitschr. f. Biol. II., 1866 ; *M. Schultze*, Observationes, &c., Bonn, 1868 ; *Babuchin*, in Med. Centralbl., 1868 ; *S. Mayer*, Bau d. sympath. Nervensyst., Wiener Sitzungsb., 1878 ; *Ranvier*, in Arch. de physiol., 1872; Tubes nerveux en T, Compt. rend. LXXI. ; and Leçons sur l'hist. du système nerv., 1878 ; *Gerlach*, Structur der grauen Substanz, Med. Centralbl., 1872 ; *Lantermann*, in Med. Centralbl., 1874, and Arch. f. mikr. Anat. XII., 1876 ; *Boll*, Hist. d. nerv. Centralorg., Arch. f. Psych., 1873 ; *McCarthy*, On spinal ganglia and nerve-fibres, Qu. J. of Micr. Sci., 1876 ; *Key & Retzius*, Studien in d. Anat. d. Nervensyst., &c., 1876 ; *H. D. Schmidt*, in Monthly Microsc. Journal, XI. ; *Kuhnt*, in Arch. f. mikr. Anat. XIII., 1876 ; *Ewald u. Kühne*, Ue. einem neuen Bestandth. d. Nervensyst., Heidelb. Verhandl., I. 1877 ; *Rumpf*, in Heidelberg Unters., II., 1878 ; *Frend*, Ue. Spinalgangl. d. Petromyzon, Wiener Sitzungsb., 1878 ; *H. Schultze*, in Arch. f. Anat. (u. Phys.), 1878 ; *Hesse*, in Arch. f. Anat. (u. Phys.), 1878 ; *Koch*, Dissert., Erlangen, 1879 ; *G. Retzius*, On nerve-cells of spinal ganglia, in Nord. med. Ark., 1880 ; *Rawitz*, Bau der Spinalganglien, Arch. f. mikr. Anat., 1880 ; and die Ranvier'sche Einschnurungen, &c., Arch. f. Anat. (u. Phys.), 1879 ; *Stricker u. Unger*, in Wiener Sitzungsb., 1879 ; *Engelmann*, Discontinuität d. Axencylinders, Pflüger's Arch. XXII., 1880 ; *Pertick*, in Arch. f. mikr. Anat., 1880.

On Development of Nerves.—*Hensen*, in Virch. Arch., XXX. & XXXI., 1864, and Arch. f. mikr. Anat. IV., 1868 ; *Eberth*, in Arch. f. mikr. Anat., II., 1866 ; *Rouget*, in Comptes rendus, LXXIX., 1873 ; *Flechsig*, Die Leitungsbahnen im Gehirn u. Ruckenmark, 1876 ; *Leboucq*, in Bull. d. l'acad. de Belgique, 1876.

On Degeneration and Regeneration of Nerves.—*Laveran*, in J. de l'anat., V. ; *E. Neumann*, in Arch. d. Heilkunde, IX. ; and Arch. f. mikr. Anat., XVIII., 1880 ; *Herz*, in Virch. Archiv, XLVI., 1869 ; *W. Krause*, in Arch. f. Anat., 1870 ; *Engelmann*, in Pfl. Arch., XIII., 1876 ; *Ranvier*, Leçons, 1878 ; and in Compt. rend., LXXVIII., 1879 ; *S. Mayer*, in Wiener Sitzungsb., 1878 ; *Rumpf*, in Heidelb. Unters., II., 1878.

On the Endings of Motor Nerves.—*Rouget*, in Comptes rendus, LV., 1862 ; LIX., 1864 ; *W. Krause*, several papers in Göttinger Nachr., Zeitschr. f. rat. Med., and Arch. f. Anat. ; and "Motor. Endplatten," 1869 ; *Kühne*, Periph. Endorg. d. motor. Nerven, 1862 ; various papers in Virch. Arch. ; and article in Stricker's Handb., 1871 ; *Waldeyer*, in Med. Centralbl., 1863 ; *Cohnheim*, in Virch. Arch., XXXIV., 1865 ; *J. Gerlach*, Verhältn. d. Nerven, &c., Leipzig, 1874 ; *Ranvier*, in Leçons, &c., 1878 ; *Schwalbe*, Gesetz des Muskel-nerveneintritts, Arch. f. Anat. (u. Phys.), 1879.

Nerves of Non-striated Muscle.—*Klebs*, in Med. Centralbl., 1863, and Virch. Arch., XXXII., 1864 ; *Frankenhausen*, in Med. Centralbl., 1866 ; *Tolotschinoff*, in Arch. f. mikr. Anat. V., 1869 ; *Arnold*, article "Organ. Muskeln," in Stricker's Handb., 1871 ; *Löwit*, in Wiener Sitzungsb., 1875.

A complete list of books and papers treating of the peripheral distribution and modes of termination of sensory nerves will be found in the work by Merkel "Ueber die Endigungen der sensiblen Nerven, &c.," Rostock, 1880. To the list there given may be added—*Krause*, in Arch. f. mikr. Anat. XIX., 1880, *Flemming* in same journal ; *Ranvier*, in Qu. J. Micr. Sci., 1880 (nerves in epidermis) ; and *Klein* in same journal (nerves of cornea). The following treat of the nerve-endings in tendon :—*C. Sachs*, in Arch. f. Anat., 1875 ; *Rollett*, in Wiener Sitzungsb., 1876 ; *Golgi*, in Atti. d. soc. di scienze nat. a Milano, XXI., 1879.

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* According to S. Mayer, degeneration of nerve-fibres, followed by their regeneration, is constantly found to occur as a normal process, without artificial severance from the nutritive centre. Mayer conceives that in this way the nerve-fibres throughout the body are continually being renewed.

BLOOD-VESSELS.

The blood, from which the solid textures immediately derive material for their nourishment, is conveyed through the body by branched tubes named blood-vessels. It is driven along these channels by the action of the heart, which is a hollow muscular organ placed in the centre of the sanguiferous system. One set of vessels, named *arteries,* conducts the blood out from the heart and distributes it to the different regions of the body, whilst other vessels named *veins* bring it back to the heart again. From the extreme branches of the arteries the blood gets into the commencing branches of the veins or revehent vessels, by passing through a set of very fine tubes which connect the two, and which, though not abruptly or very definitely marked off from either, are generally spoken off as an intermediate set of vessels, and by reason of their smallness are called the *capillary* (*i.e.,* hair-like) *vessels,* or, simply, the *capillaries.*

ARTERIES.

These vessels were originally supposed to contain air. This error, which had long prevailed in the schools of medicine, was refuted by Galen, who showed that the vessels called arteries, though for the most part found empty after death, really contain blood in the living body.

Mode of Distribution.—The arteries usually occupy protected situations; thus, after coming out of the great visceral cavities of the body, they run along the limbs on the aspect of flexion, and not upon that of extension where they would be more exposed to accidental injury.

As they proceed in their course the arteries divide into branches, and the division may take place in different modes. An artery may at once resolve itself into two or more branches, no one of which greatly exceeds the rest in magnitude, or it may give off several branches in succession and still maintain its character as a trunk. The branches come off at different angles, most commonly so as to form an acute angle with the further part of the trunk, but sometimes a right or an obtuse angle, of which there are examples in the origin of the intercostal arteries.

An artery, after a branch has gone off from it, is smaller than before, but usually continues uniform in diameter or cylindrical until the next secession; thus it was found by Hunter that the long carotid artery of the camel does not diminish in calibre throughout its length. A branch of an artery is less than the trunk from which it springs, but the combined area or collective capacity of all the branches into which an artery divides, is greater than the calibre of the parent vessel immediately above the point of division. The increase in the joint capacity of the branches over that of the trunk is not in the same proportion in every instance of division, and there is at least one case known in which there is no enlargement, namely, the division of the aorta into the common iliac and sacral arteries; still, notwithstanding this and other possible exceptions, it must be admitted as a general rule that an enlargement

of area takes place. From this it is plain that, since the area of the arterial system increases as its vessels divide, the capacity of the smallest vessels and capillaries will be greatest; and, as the same rule applies to the veins, it follows that the arterial and venous systems may be represented, as regards capacity, by two cones whose apices (truncated it is true) are at the heart, and whose bases are united in the capillary system. The effect of this must be to make the blood move more slowly as it advances along the arteries to the capillaries, like the current of a river when it flows in a wider and deeper channel, and to accelerate its speed as it returns from the capillaries to the venous trunks.

When arteries unite they are said to anastomose or inosculate. Anastomoses may occur in tolerably large arteries, as those of the brain, the hand and foot, and the mesentery, but they are much more frequent in the smaller vessels. Such inosculations admit of a free communication between the currents of blood, and must tend to promote equability of distribution and of pressure, and to obviate the effects of local interruption.

Arteries commonly pursue a tolerably straight course, but in some parts they are tortuous. Examples of this in the human body are afforded by the arteries of the lips and of the uterus, but more striking instances may be seen in some of the lower animals, as in the well-known case of the long and tortuous spermatic arteries of the ram and the bull. In very moveable parts like the lips, this tortuosity will allow the vessel to follow their motions without undue stretching; but in other cases its purpose is not clear. The physical effect of such a condition of the vessel on the blood flowing along it must be to reduce the velocity, by increasing the extent of surface over which the blood moves, and consequently the amount of impediment from friction; still it does not satisfactorily appear why such an end should be provided for in the several cases in which arteries are known to follow a tortuous course. The same remark applies to the peculiar arrangement of vessels named a "rete mirabile," where an artery suddenly divides into small anastomosing branches, which in many cases unite again to re-construct and continue the trunk. Of such *retia mirabilia* there are many examples in the lower animals, but, as already remarked, the purpose which they serve is not apparent. The best known instance is that named the *rete mirabile of Galen,* which is formed by the intra-cranial part of the internal carotid artery of the sheep and several other quadrupeds.

Arteries possess considerable strength and a very high degree of elasticity, being extensible and retractile both in their length and their width. When cut across they present, although empty, an open orifice; the veins, on the other hand, collapse, unless when prevented by connection with surrounding rigid parts.

Structure.—In most parts of the body the arteries are inclosed in a sheath formed of connective tissue, and their outer coat is connected to the sheath by filaments of the same tissue, but so loosely that, when the vessel is cut across, its ends readily shrink some way within the sheath. Some arteries want sheaths, as those for example which are situated within the cavity of the cranium.

Independently of this sheath, arteries (except those of minute size whose structure will be afterwards noticed with that of the capillaries)

have been usually described as formed of three coats, named, from their relative position, internal, middle, and external (fig. 178, in section); and as this nomenclature is generally followed in medical and surgical

Fig. 178.

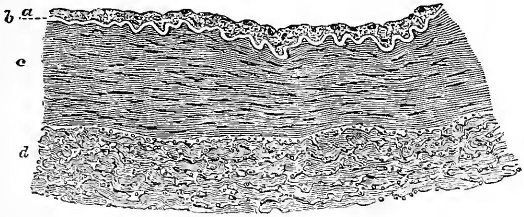


Fig. 178.—Transverse section of part of the wall of the posterior tibial artery (man). 75 diameters. (E.A.S.)

a, Epithelial and subepithelial layers of inner coat; *b*, elastic layer (fenestrated membrane) of inner coat, appearing as a bright line in section; *c*, muscular layer (middle coat); *d*, outer coat, consisting of connective tissue bundles. In the interstices of the bundles are some connective tissue nuclei, and, especially near the muscular coat, a number of elastic fibres cut across.

works, and also correctly applies to the structure of arteries so far as it is discernible by the naked eye, it seems best to adhere to it as the basis of our description; although it will be seen, as we proceed, that some of these coats are found on microscopic examination really to consist of two or more strata differing from each other in texture, and therefore reckoned as so many distinct coats by some authorities.

Internal coat (*Tunica intima*) (fig. 178, *a*, *b*). This may be raised from the inner surface of the arteries as a fine transparent colourless membrane, elastic but very easily broken, especially in the circular or transverse direction, so that it cannot be stripped off in large pieces. It is very commonly corrugated with fine and close longitudinal wrinkles,

Fig. 179.

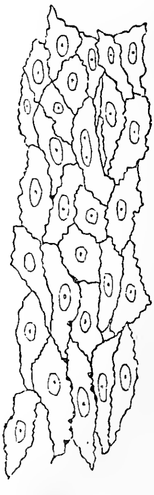


Fig. 179.—Epithelial layer lining the posterior tibial artery of man. 250 diameters. (E.A.S.)
Nitrate of silver preparation.

caused most probably by a contracted state of the artery after death. Such is the appearance presented by the internal coat to the naked eye, but by the aid of the microscope, it is found to consist of three different structures, namely:—

1. An *epithelial layer* (fig. 178, *a*, and fig. 179) forming the innermost part or lining. This is a simple layer of thin elliptical or irregularly polygonal cells, which are often lengthened into a lanceolate shape. The cells have round or oval nuclei, with nucleoli: their outlines are often indistinct in the fresh state, but may be brought into view by means of nitrate of silver.

2. A *subepithelial layer* (striated layer of Kölliker). This is composed of a finely fibrillated connective tissue with a number of branched corpuscles lying in the cell-spaces of the tissue (fig. 180). This layer is most developed in the larger arteries: it exists however in the medium-sized ones. In the aorta it is very well marked and contains a large number of anastomosing cells and cell-spaces lying on a finely fibrillated ground-substance. Moreover, longitudinal networks of very fine elastic fibres, which are in continuity with the larger elastic fibres of the next layer, occur in it in the aorta.

Fig. 180.

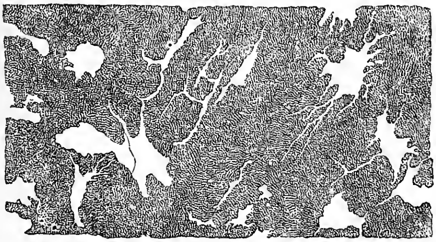


Fig. 180.—Cell-spaces of subepithelial layer of artery (posterior tibial). 250 diameters. (E.A.S.)

The ground substance is stained by nitrate of silver, and the cell-spaces of the tissue are thus made manifest as white patches, the contained cells not being seen.

3. *Elastic layers* (fig. 178, *b*). These form the chief substance of the inner coat. The elastic tissue forms longitudinal networks of fibres (fig. 181), which consist of one or more layers of different degrees of closeness. Not uncommonly some of these (or one in particular) take on a membranous character, in which case the "perforated" or "fenestrated" membrane of Henle is formed. This consists of a thin and brittle transparent film of elastic tissue. It can be stripped off in small shreds, which have a remarkable tendency to curl in at their borders, and roll themselves up as represented in fig. 182. The films of membrane are marked by fine pale lines, following principally

Fig. 181.

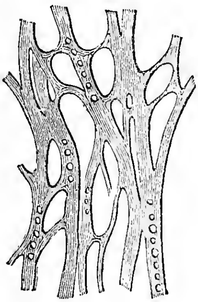


Fig. 182.

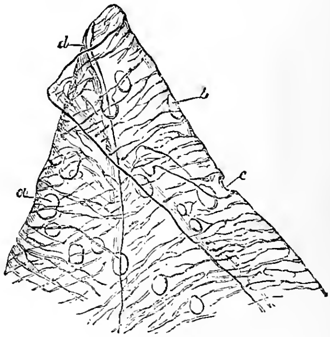


Fig .181.—Elastic network of artery. 250 diameters (Kölliker).

Fig. 182.—Portion of fenestrated membrane from the femoral artery, magnified 200 diameters (Henle).

a, *b*, *c*, perforations.

a longitudinal direction, and joining each other obliquely in a sort of network. These lines are reticulating fibres formed upon the membranous layer and continuous with the reticulating elastic fibres which pervade the muscular coat on the one side and with those which extend into the subepithelial layer on the other. The membrane is further remarkable by being perforated with numerous round, oval, or irregularly shaped apertures of different sizes. In some parts of the arteries the perforated membrane is very thin, and therefore difficult to strip off; in other situations it is of considerable thickness, consisting of several layers; in which case it tends in the outer layers to lose its membranous character: indeed it must be borne in mind that every transition is met with between the fenestrated membranes, and the longitudinal elastic network.

The inner coat may thus be said to be formed of (1) a layer of flattened epithelial cells, (2) a layer of delicate connective tissue with branched cells; and (3) of elastic tissue under two principal forms, namely, the longitudinal elastic networks and the fenestrated membrane; and these two forms may coexist in equal amount, or one may predominate, the other diminishing or even disappearing altogether.

Middle coat (*Tunica media*) (fig. 178, *c*). This consists of plain muscular tissue, in fine bundles, disposed circularly round the vessel, and consequently tearing off in a circular direction, although the individual bundles do not form complete rings. The considerable thickness of the walls of the larger arteries is due chiefly to this coat; and in the smaller

Fig. 183.

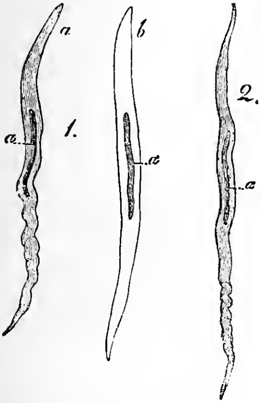


Fig. 184.

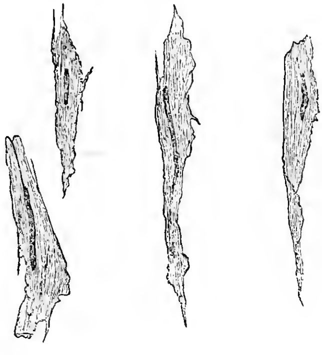


Fig. 183.—Muscular fibre-cells from human arteries. Magnified 350 diameters.

1. From the popliteal artery; *a*, natural; *b*, treated with acetic acid. 2, From a small branch of the posterior tibial (from Kölliker).

Fig. 184.—Muscular fibre-cells from superior thyroid artery (man). 340 diameters. (E.A.S.)

ones, it is said to be thicker in comparison with the calibre of the vessel. In the larger vessels it is made up of many layers; and elastic films either finely reticular, or quite similar to the fenestrated membrane of the inner coat, are found between the muscular layers alternating with them, and also being united with one another by elastic fibres passing between the muscular bundles. In most arteries this elastic tissue of the

middle coat is but slightly developed, but in the aorta (fig. 183) and carotid arteries and in some of the branches of the latter, it attains a considerable development, and since in them also elastic fibres are seen extending into the subepithelial layer of the inner coat, the distinction between the inner and middle coats as shown in section is far less marked than it is in ordinary arteries. The middle coat is of a tawny or reddish yellow colour, not unlike that of the elastic tissue, but, when quite fresh, it has a softer and more translucent aspect. Its internal part is often described as redder than the rest, but the deeper tint is probably due to staining by the blood after death.

The muscular fibre-cells of the middle coat of the arteries (fig. 183 and fig. 184) are seldom more than from $\frac{1}{300}$ to $\frac{1}{200}$ of an inch long and frequently, especially in those arteries in which the elastic tissue of the middle coat is most developed, present a very irregular shape with jagged extremities (fig. 184). Their nuclei are distinctly rod-shaped and are often slightly curved.

Bundles of white connective-tissue fibrils may also occur in small quantity in the middle coat, the proportion increasing with the size of the artery. It is important to note that the muscular tissue of the middle coat is more pure in the smaller arteries, and that the admixture of other tissues increases in the larger-sized vessels ; in these, moreover, the muscular cells are smaller. Accordingly, the contractility of the arteries, which depends on their middle coat, is little marked in those of large size, but becomes much more conspicuous in the smaller branches.

External coat (*Tunica adventitia*) (fig. 178, *d*). This is composed mainly of fine and closely-felted bundles of white connective tissue, together with a variable amount of longitudinally disposed elastic tissue between the bundles (in the figure this is seen cut across). The latter is much more abundant towards the inner part, next the muscular coat, and is frequently described as constituting here a distinct elastic layer : it is most marked in arteries of medium calibre, becoming thinner, and at length gradually disappearing in those of small size.

In large and middle-sized arteries the bundles of white connective tissue chiefly run diagonally or obliquely round the vessel, and their interlacement becomes much more open and lax towards the surface of the artery, where they connect the vessel with its sheath or with other surrounding parts. Longitudinally arranged contractile fibre-cells have been described by various observers in the external coat of some of the larger arteries (especially the iliacs, superior mesenteric, splenic, renal and dorsalis penis, and in the umbilical arteries of the fœtus). In the umbilical arteries, according to Eberth, a complete layer of longitudinal muscular fibres is also present in the middle coat, internal to the ordinary circular fibres. Scattered longitudinal muscular cells are present in some arteries amongst the circularly disposed fibres of the middle coat, and even in the subepithelial layer of the internal coat. The outer coat is usually of greater proportionate thickness in the smaller arteries, but as it shades off into the surrounding connective tissue it is difficult to adjudge its exact thickness.

Some arteries have much thinner coats than the rest, in proportion to their calibre. This is strikingly the case with those contained within the cavity of the cranium, and in the vertebral canal ; the difference depends on the external and middle coats, which in the vessels referred to are thinner than elsewhere.

Vessels and Nerves of Arteries.—The coats of arteries receive small vessels, both arterial and venous, named *vasa vasorum,* which serve for their nutrition. The little nutrient arteries are not derived immediately from the cavity of the main vessel but pass into its coats from branches which arise from the artery (or sometimes from a neighbouring artery), at some distance from the point where they are ultimately distributed, and divide into smaller branches within the sheath, and upon the surface of the vessel, before entering the outer coat where they are distributed. In some of the larger mammals, a few pass into the middle coat, and follow the circular course of its fibres, but in health none penetrate into this coat in the human subject and still less into the internal coat (Ranvier). Minute venules return the blood from these nutrient arteries, which, however, they do not closely accompany, and discharge it into the vein or pair of veins which usually runs alongside the artery. Lymphatics are present in the outer coat.

Arteries are generally accompanied by larger or smaller nerves; and when, in the operation of tying an artery, these happen to be included along with it in the ligature, pain is experienced; but the vessel itself, when in a healthy condition, is insensible. Nerves are, nevertheless, distributed to the coats of arteries. They form plexuses round the larger arteries, and run along the smaller branches in form of fine bundles of fibres, which here and there twist round the vessel, and unite with one another in a plexiform manner. The fine branches destined for the artery penetrate to the middle coat, to the muscular tissue of which they are chiefly distributed.

Minute ganglia are found in various parts connected with the arteries, but their existence does not appear to be by any means universal.

VEINS.

Mode of distribution.—The veins are ramified throughout the body, like the arteries, but in most regions and organs of the body they are more numerous and larger, so that the venous system is altogether more capacious than the arterial. The pulmonary veins form an exception to this rule, for they do not exceed in capacity the pulmonary arteries.

The veins are arranged in a superficial and a deep set, the former running immediately beneath the skin, and thence named subcutaneous, the latter usually accompanying the arteries, and named *venæ comites vel satellites arteriarum.* The large arteries have usually one accompanying vein, and the medium-sized and smaller arteries two, but there are exceptions to this rule. The veins within the skull and spinal canal, the hepatic veins, and the most considerable of those belonging to the bones, run apart from the arteries.

The communications or anastomoses between veins of considerable size, are more frequent than those of arteries of equal magnitude.

Structure.—The veins have much thinner coats than the arteries, and collapse when cut across or emptied; whereas a cut artery presents a patent orifice. But, notwithstanding their comparative thinness, the veins possess considerable strength, more even, according to some authorities, than arteries of the same calibre. The number of their coats has been differently reckoned, and the tissues composing them differently described by different writers, and this discrepancy of statement is perhaps partly due to the circumstance that all veins are not perfectly

alike in structure. In most veins of moderate size, three coats may be distinguished, which, as in the arteries, have been named external, middle, and internal.

Internal coat.—This is less brittle than that of the arteries, and therefore admits of being more readily peeled off without tearing; but, in other respects, the two are much alike. It consists of an *epithelium*, a *subepithelial connective tissue layer*, and an *elastic layer* (fig. 185, *a*, *b*).

The epithelium of the veins is similar in character to that of the arteries, but the cells are shorter and broader. The subepithelial layer is less developed in most veins than in the arteries, and indeed is absent altogether in many. It is better marked in some of the medium-sized veins than in the larger trunks. The elastic tissue of the inner coat occurs as dense lamelliform networks of longitudinal elastic fibres, and

Fig. 185.

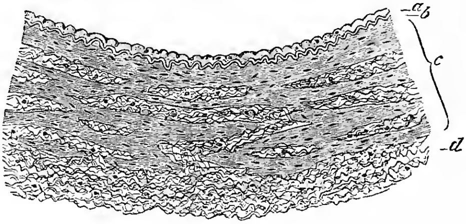


Fig. 185.—Transverse section of part of the wall of one of the posterior tibial veins (man). (E. A. S.)

a, Epithelial and subepithelial layers of inner coat; *b*, elastic layers of inner coat; *c*, middle coat consisting of irregular layers of muscular tissue, alternating with connective tissue, and passing somewhat gradually into the outer connective tissue and elastic coat, *d*.

but seldom as fenestrated membranes. Longitudinal muscular bundles, as well as isolated contractile cells, are found in the inner coat of some veins.

Middle coat.—This tunic is thinner than that of the arteries, and has a much larger admixture of white connective tissue. It is pervaded by an elastic network, but this is even less conspicuous in the veins than in the arteries. In the veins of the limbs (especially the upper) and in those of some other parts, the muscular fibre-cells have for the most part as in the arteries a transverse direction, although the layer which they form is not everywhere complete, being separated into bundles by the intervention of connective tissue (fig. 185, *c*). But in many veins some of the innermost fibres of the middle coat take a longitudinal course. This is the case with the iliac, crural, branches of the mesenteric, umbilical of the fœtus, and other veins (Eberth).

In many of the larger veins the middle coat is less developed, especially as regards its muscular fibres, but in such cases the deficiency may be supplied by muscularity of the outer coat. The middle coat is wanting altogether in the thoracic part of the inferior vena cava, but is well marked in the hepatic part: in the part below the liver the muscularity of the middle coat is less marked. In the internal and external jugular veins there is but a slight development of the muscular tissue.

External coat (fig. 185, *d*).—This is often thicker than the middle

coat; but the line of junction between them is not sharply marked. It consists of dense areolar tissue and longitudinal elastic fibres. In certain large veins, as pointed out by Remak, this coat contains a considerable amount of plain or non-striated muscular tissue. Thus the muscular elements are well marked in the whole extent of the abdominal cava, in which they form a longitudinal network, occupying the inner part of the external coat; and they may be traced into the renal, azygos, spermatic and external iliac veins. The muscular tissue of the external coat is also well developed in the trunks of the hepatic veins and in that of the vena portæ, whence it extends into the splenic and superior mesenteric. It is found also in the axillary vein.

Other veins present peculiarities of structure, especially in respect of muscularity, as follows. 1. The striated muscular tissue of the auricles of the heart is prolonged for some way on the adjoining part of the venæ cavæ and pulmonary veins. 2. The (plain) muscular tissue is largely developed in the veins of the gravid uterus, in which, as well as in some other veins, it is described as being present in all three coats, and as having for the most part a longitudinal arrangement. 3. On the other hand, muscular tissue is wanting in the following veins, viz., *a*, those of the maternal part of the placenta; *b*, most of the veins of the pia mater; *c*, the veins of the retina; *d*, the venous sinuses of the dura mater; *e*, the cancellar veins of the bones; *f*, the venous spaces of the corpora cavernosa. In most of these cases the veins consist merely of an epithelium and a layer or layers of connective tissue more or less developed; in the corpora cavernosa the epithelium is applied to the trabecular tissue. It may be added that in the thickness of their coats the superficial veins surpass the deep, and the veins of the lower limbs those of the upper.

The coats of the veins are supplied with nutrient vessels, *vasa vasorum*, in the same manner as those of the arteries. Nerves are distributed to them in the same manner as to the arteries, but in far less abundance.

Valves.—Most of the veins are provided with valves, a mechanical contrivance adapted to prevent the reflux of the blood. The valves are formed of semilunar folds of the internal coat, strengthened by included

Fig. 186.

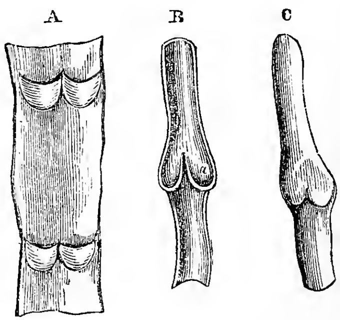


Fig. 186.—Diagram showing valves of veins.

A. Part of a vein laid open and spread out, with two pairs of valves. B. Longitudinal section of a vein, showing the apposition of the edges of the valves in their closed state. C. Portion of a distended vein, exhibiting a swelling in the situation of a pair of valves.

connective tissue, and projecting into the vein. Most commonly two such folds or flaps are placed opposite each other (fig. 186, A); the convex border of each (which, according to Haller, forms a parabolic curve) is connected with the side of the vein; the other edge is free, and points towards the heart, or at least in the natural direction of the current of the blood along the vessel, and the two flaps incline obliquely

towards each other in this direction. Moreover the wall of the vein immediately on the cardiac side of the curved line of attachment of the valves, is dilated into a pouch or *sinus* (fig. 186, B), so that, when distended with blood or by artificial injection, the vessel bulges out on each side, and thus gives rise to the appearance of a knot or swelling wherever a valve is placed (as in fig. 186, C). From the above description, it is plain that the valves are so directed as to offer no obstacle to the blood in its onward flow, but that, when from pressure or any other cause it is driven backwards, the refluent blood, getting between the dilated wall of the vein and the flaps of the valve, will press them inwards until their edges meet in the middle of the channel and close it up.

The epithelium-cells differ in shape and arrangement upon the two surfaces of the valves. On the side which faces inwards, and past which the current of blood flows, the cells are elongated in the direction of the current, whereas upon the opposite side which, when the valves are thrown back, faces the wall of the vein, the cells are elongated transversely. The main substance of the valve is formed by bundles of connective tissue, which have for the most part a transverse arrangement, and between which a few elastic fibres are seen. The tissue is covered on each surface by a prolongation of the inner coat of the vein, the covering being much thicker on the inner than on the outer surface. The valve is thinner close to its attachment than elsewhere. At its base a few transverse muscular fibres are sometimes seen, prolonged into it from the middle coat.

The valvular folds are usually placed in pairs as above described; in the veins of the horse and other large quadrupeds three are sometimes found ranged round the inside of the vessel; but this rarely occurs in the human body. On the other hand, the folds are placed singly in some of the smaller veins, and in large veins single valvular folds are not unfrequently placed over the openings of smaller entering branches; also in the right auricular sinus of the heart there is a single crescentic fold at the orifice of the vena cava inferior, and another more completely covering the opening of the principal coronary vein.

Many veins are destitute of valves. Those which measure less than $\frac{1}{12}$th of an inch (about 2 millimeters) in diameter rarely, if ever, have them. In man, valves are wanting in the superior and inferior venæ cavæ, in the trunk and branches of the portal vein, in the hepatic, renal, and uterine veins; also in the spermatic (ovarian) veins of the female. In the male, these last-mentioned veins have valves in their course, and in each sex a little valve is occasionally found in the renal vein, placed over the entrance of the spermatic. The pulmonary veins, those within the cranium and vertebral canal, and those of the cancellated texture of bone, as well as the trunk and branches of the umbilical vein, are also without valves. In the azygos and intercostal veins valves are not generally found, and when present are few in number. On the other hand, they are numerous in the veins of the limbs (and especially of the lower limbs), which are much exposed to pressure in the muscular movements or from other causes, and have often to support the blood against the direction of gravity. No valves are met with in the veins of reptiles and fishes, and not many in those of birds.

SMALLER ARTERIES AND VEINS AND CAPILLARIES.

That the blood passes from the extreme arteries into the veins was a necessary part of the doctrine of the circulation, as demonstrated by Harvey, in 1628; but the mode in which the passage takes place was not ascertained until some time after the date of his great discovery. The finding of the capillary vessels, and of the course of the blood

through them, was in fact one of the first fruits of the use of the microscope in anatomy and physiology, and was reserved for Malpighi (in 1661).

When the web of a frog's foot is viewed through a microscope of moderate power (as in fig. 187), the blood is seen passing rapidly along the small arteries, and thence more slowly through a network of finer channels, by which it is conducted into the veins. These small vessels interposed between the finest branches of the arteries and the commencing veins, are the capillary vessels. The course of the blood in them may be conveniently seen also in the lungs or mesentery of the frog, in the external gills and tail of tadpoles ; in the tail of small fishes ; in the mesentery of small quadrupeds ; and generally, in short, in the transparent vascular parts of animals which can be brought under the microscope. These vessels can also be demonstrated by means of fine injections of coloured material, not only in membranous parts, such as those above mentioned, but also in more thick and opaque tissues, which can be subsequently rendered transparent.

Fig. 187.

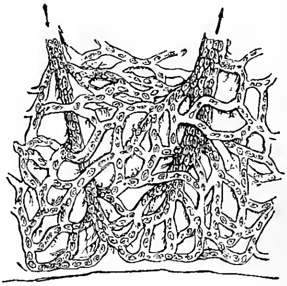


Fig. 187.—Capillary blood-vessels in the web of a frog's foot, as seen with the microscope (after Allen Thomson).

The arrows indicate the course of the blood.

The capillary vessels of a part are most commonly arranged in a network, the branches of which are of nearly uniform size, though not all strictly equal ; and thus they do not divide into smaller branches like the arteries, or unite into larger ones like the veins ; but the diameter of the tubes, as well as the shape and size of the reticular meshes which they form, differs in different textures. Their prevalent size in the human body may, speaking generally, be stated at from $\frac{1}{3500}$ to $\frac{1}{2000}$ of an inch, as measured when naturally filled with blood. But they are said to be in some parts considerably smaller, and in others larger than this standard : thus, Weber measured injected capillaries in the brain, which he found to be not wider than $\frac{1}{4700}$ of an inch, and Henle has observed some still smaller,—in both cases apparently smaller than the natural diameter of the blood-corpuscles. The capillaries, however, when deprived of blood, probably shrink in calibre immediately after death ; and this consideration, together with the fact that their distension by artificial injection may exceed or fall short of what is natural, should make us hesitate on such evidence to admit the existence of vessels incapable of permitting the red corpuscles of the blood easily to pass through them. The diameter of the capillaries of the marrow of the bones is stated to be $\frac{1}{1200}$ of an inch. In other parts, their size varies between the extremes mentioned : it is small in the lungs, and in muscle ; larger in the skin and mucous membranes. The extreme branches of the arteries and veins in certain parts of the synovial membranes are connected by capillary loops, which are considerably dilated at their point of flexure, and dilatations are also found upon the transverse capillaries of the red muscles of the rabbit.

There are differences also in the size or width of the meshes of the

capillary network in different parts, and consequently in the number of vessels distributed in a given space, and the amount of blood supplied to the tissue. The network is very close in the lungs and in the choroid coat of the eye, and comparatively close in muscle, in fat, in the skin, and in most mucous membranes, also in glands and secreting structures, and in the grey part of the brain and spinal cord. On the other hand, it has wide meshes and comparatively few vessels in the ligaments, tendons, and other allied textures. In infants and young persons, the tissues are comparatively more vascular than in after-life.

The figure of the capillary network is not the same in all textures. In many cases the shape of the meshes seems accommodated to the arrangement of the elements of the tissue in which they lie. Thus in muscle, nerve, and tendon, the meshes are long and comparatively narrow, and run conformably with the fibres and fasciculi of these textures. In other parts, as in the lungs, in fat, and in secreting glands, the meshes are rounded or polygonal, with no one dimension greatly predominating. In the papillæ of the skin and mucous membranes, the vessels of the network are often drawn out into prominent simple or ramified loops.

The smallest arteries and veins pass by gradual transition into the capillary vessels, and their finest offsets approach very near to these in structure; these may therefore be conveniently considered along with the capillary vessels.

Structure of the capillaries.—The wall of the capillaries proper is formed entirely of a simple epithelial layer, composed of flattened lanceolate cells joined edge to edge, and continuous with the corresponding layer which lines the arteries and veins. The outlines of the cells or their lines of junction one with another may be made apparent by nitrate of silver (fig. 188); while the nuclei, which show a well-marked network of nucleoplasm, may be brought into view by logwood or carmine. Commonly there are not more than two or three such cells in the cross section of a capillary. At the points of junction of the capillaries the cells are usually broader and not spindle-shaped, but radiate, with three or four pointed branches fitting in between the cells of the three or four adjoining vessels which meet at the spot (fig. 188, *c*, *c*, *c′*).

Fig. 188.

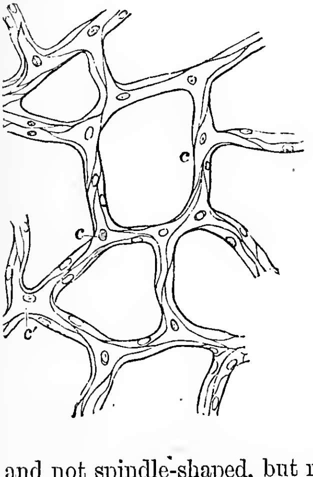


Fig. 188.—Capillary vessels from the bladder of the cat, magnified (after Chrzonszczewsky.)

The outlines of the cells are stained by nitrate of silver.

In capillaries which have been submitted to the action of nitrate of silver, there is here and there to be seen between the cells of the capillary wall an increase in amount of the intercellular substance, appearing as an enlargement of the fine line of the silver deposit. To these gaps in the capillary wall, which however are closed by intercellular substance, J. Arnold has applied the term "stigmata;" they are analogous to the "pseudo-stomata" found between the epithelium cells of a

serous membrane. It is probable that the white blood corpuscles, when migrating from the blood-vessels, pass between the epithelium-cells, especially in the situation of the stigmata.

Branched cells of the surrounding areolar tissue are found connected intimately with the cells forming the capillary wall. This connection occurs almost everywhere, but it is more obvious in parts which are pervaded by a supporting network of retiform connective tissue, such as the substance of the

Fig. 189.

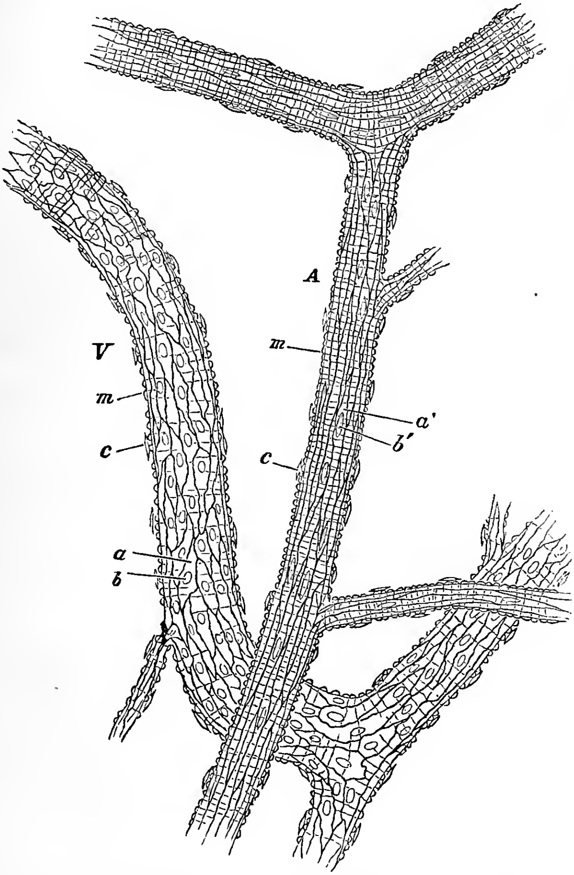


Fig. 189.—A SMALL ARTERY A, AND VEIN V, FROM THE SUBCUTANEOUS CONNECTIVE TISSUE OF THE RAT. TREATED WITH NITRATE OF SILVER. 175 DIAMETERS (E.A.S.).

a, *a′*, epithelium-cells with *b*, *b′*, their nuclei; *m*, *m*, transverse markings due to staining of substance between the muscular fibre-cells; *c*, *c*, nuclei of connective tissue corpuscles attached to exterior of vessel.

lymphatic glands, the solitary and agminated intestinal glands and adjacent mucous membrane, where the small vessels and capillaries may even obtain a continuous covering from the reticulating processes of the cells. This coating has been named by His, *adventitia capillaris*.

Outgrowths from the capillary wall have been described by Stricker as occurring not only in the progress of development, in the manner to be afterwards detailed, but also in the fully developed capillaries of the frog; and contraction both of

the whole capillary wall and also of the individual cells of young capillary vessels has also been described (Stricker, Tarchanoff), but it is not known whether the walls of the capillaries of the adult mammal possess any appreciable contractility.

Structure of the small arteries and veins.—In vessels a little larger than the capillaries, there is added outside the epithelial layer (fig. 189, *a*, *a′*), a layer of plain muscular tissue, in form of the usual long contractile fibre-cells, which are directed across the length of the vessel (fig. 189, *m*, *m*). The elongated nuclei of these cells may be brought into view by means of acetic acid or by staining fluids. This layer corresponds with the middle coat of the larger vessels. In the smallest vessels in which it appears the muscular cells are few and apart, and a single long cell may turn spirally round the tube (Lister); in larger vessels, especially those of the arterial system, the muscular cells are more closely arranged. Outside the muscular coat is the areolar or connective tissue coat, containing fibres and connective tissue corpuscles, with longitudinally placed nuclei.

In vessels of $\frac{1}{60}$ of an inch in diameter, or even less, the elastic layers of the inner coat may be discovered (fig. 190, A, δ), in the form generally

Fig. 190.

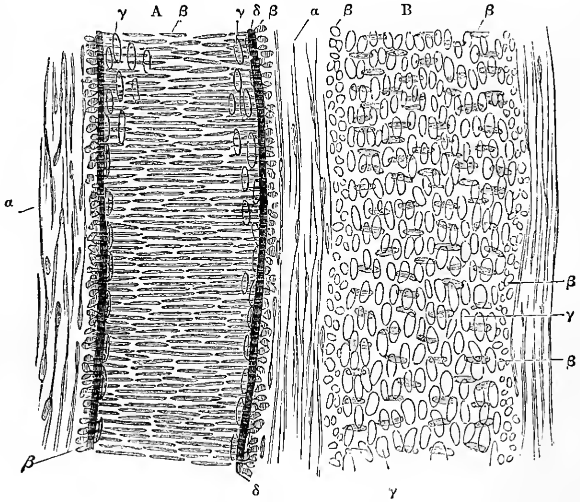


Fig. 190.—A SMALL ARTERY A, WITH A CORRESPONDING VEIN B, TREATED WITH ACETIC ACID, AND MAGNIFIED 350 DIAMETERS (after Kölliker).

α, external coat with elongated nuclei; *β*, nuclei of the transverse muscular tissue of the middle coat (when seen endwise, as at the sides of the vessel, their outline is circular); *γ*, nuclei of the epithelium-cells; *δ*, elastic layers of the inner coat.

of homogeneous or fenestrated membrane, more rarely of longitudinal reticulating elastic fibres. The small veins differ from arteries of corresponding size, chiefly in the inferior development of their muscular tissue; the lining cells of the arteries also are very much longer and narrower than those of the veins. These differences, as well as the comparative

size of corresponding vessels, are well shown in the accompanying figures (189 and 190).

The only open communication between the arteries and the veins, is by means of capillary vessels as above described, unless in the maternal part of the placenta and in the interior of erectile organs, in which small arteries may open directly into wide venous cavities without the intervention of capillaries. Moreover, in the spleen the arterial capillaries do not at once pass into the commencements of the veins, but open into the interstices of the organ, from which the minute veins collect the blood.

It is said that in certain parts small arteries may pass into small veins without the intervention of true capillaries (Sucquet, Hoyer).

Arterial glands.—At the upper end of the common carotid (*carotid gland*) and in front of the apex of the coccyx (*coccygeal gland*, Luschka), are found small solid-looking bodies of a somewhat glandular appearance, but composed almost entirely of a plexus of minute arteries, which are derived in the one case directly from the carotid, in the other from the middle sacral. The plexiform vessels are invested by one or more layers of granular polygonal cells, apparently like those found in the interstitial tissue of some other organs (testis, ovary, thyroid, supra-renal bodies), and probably modifications of the more widely distributed plasma-cells of the connective tissue. The whole is invested by connective tissue, which also penetrates between the vessels of the so-called gland, and itself contains numerous granular cells. The true nature and function of these peculiar structures is entirely unknown.

DEVELOPMENT OF BLOOD-VESSELS.

The first vessels which appear in the ovum are formed in the mesoderm, and the process subsequently goes on in the same layer and in its derivatives in all parts of the animal body. New vessels, also, are formed in the healing of wounds, in the restoration of lost parts, and in the

Fig. 191.

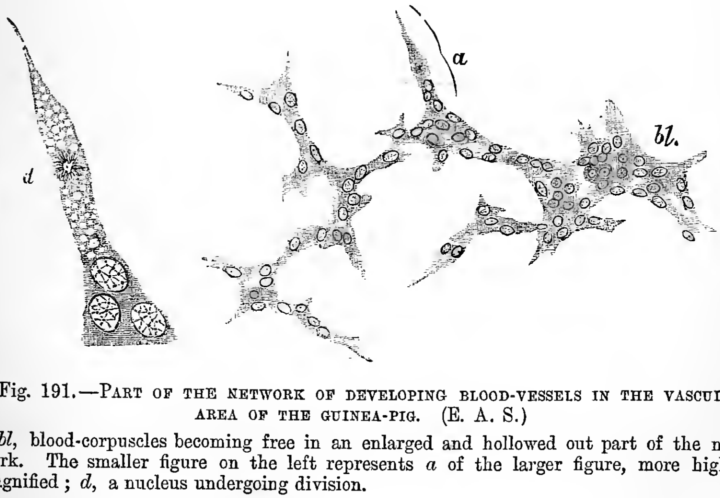


Fig. 191.—Part of the network of developing blood-vessels in the vascular area of the guinea-pig. (E. A. S.)

bl, blood-corpuscles becoming free in an enlarged and hollowed out part of the network. The smaller figure on the left represents *a* of the larger figure, more highly magnified; *d*, a nucleus undergoing division.

production of adventitious growths. The process is in every case essentially the same.

The first vessels of the embryo, both of the chick and mammal, are formed in the vascular area, and originate from some of the cells of the

mesoderm in that situation (fig. 191). Vacuoles are formed within the cells, and as they increase in size they run together, and a cavity filled with fluid is in this way produced in the interior of the cell, the nucleus of which has meanwhile become multiplied, while blood-corpuscles are formed within the cavity in the manner already described in connection with the blood (p. 34). The cells, whilst these changes are going on, increase largely in size, especially in the chick, where they form vesicles (fig. 192), visible to the naked eye as minute reddish specks, which have been known since the time of Pander as "blood-islands." The cells are united to one another by their processes, and after a time the cavities become extended into the cell-processes, so that a network of vessels is by this means produced.

Fig. 192.

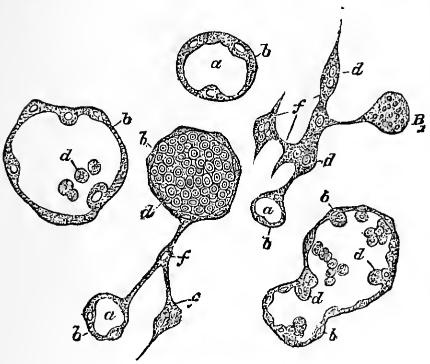


Fig. 192.—Cells from middle layer of chick's blastoderm undergoing development into blood-vessels. Magnified (from Klein).

a, cavity of cell; *b*, wall of cell; *f*, *f*, cells not yet hollowed out; *d*, blood-corpuscles.

The wall of these primary vessels is therefore composed at first merely of the protoplasm of the original embryonic cells with a few nuclei, derived by division from the original nuclei of those cells, imbedded in it here and there. Subsequently the protoplasm becomes differentiated around the nuclei into the flattened cells which compose the wall of the capillaries, and which form the lining membrane of the arteries and veins. The remaining coats of the larger vessels are developed later, from other cells which apply themselves to the exterior of the previously simple tubes and produce the plain muscular and other tissues of which those coats consist.

Within the body of the embryo, vessels are formed in like manner from cells belonging to the connective tissue. One of the most favourable objects for the study of the development of the blood-vessels and their contained blood-corpuscles is afforded by the subcutaneous tissue of the new-born rat, especially those parts in which fat is being deposited.

Here we may observe that many of the connective tissue corpuscles are much vacuolated, and that the protoplasm of some of them presents a decided reddish tinge (fig. 193, *h*). In others the red matter has become condensed in the form of globules within the cells (*h'*, *h''*, &c.), varying in size from minute specks to spheroids of the diameter of a blood-corpuscle, or more. At some parts the tissue is completely studded with these cells, each containing a number of such spheroids, and forming, as it were, "nests" of blood-corpuscles or minute "blood-islands." After a time the cells become elongated and pointed at their ends, sending out processes also to unite with neighbouring cells. At the same time the vacuoles in their interior become enlarged, and coalesce to

form a cavity within the cell (fig. 194, *a*), in which the reddish globules, which are now becoming disk-shaped (*b*), are found. Finally the cavity

Fig. 193.

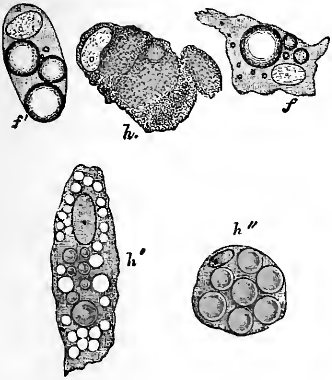


Fig. 194.

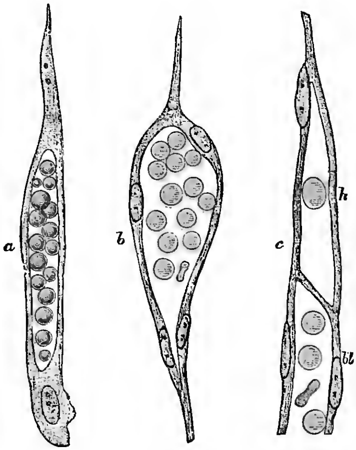


Fig. 193.—Commencing development of connective tissue cells into blood-vessels. From the subcutaneous tissue of the new-born rat. (E. A. S.)

h, a cell containing hæmoglobin in a diffused form in the protoplasm ; *h'*, one containing coloured globules of varying size, and vacuoles ; *h''*, a cell filled with coloured globules of nearly uniform size ; *f*, *f'*, developing fat cells.

Fig. 194.—Further development of connective tissue cells into capillary blood-vessels. (E. A. S.).

a, an elongated cell with a cavity in its protoplasm occupied by fluid and by blood-corpuscles which are still globular ; *b*, a hollow cell the nucleus of which has multiplied. The new nuclei are arranged around the wall of the cavity, the corpuscles in which have now become discoid ; *c*, shows the mode of union of a "hæmapoietic" cell, which in this instance contains only one corpuscle, with the prolongation (*bl*) of a previously existing vessel. *a*, and *c*, from the new-born rat ; *b*, from the fœtal sheep.

Fig. 195.

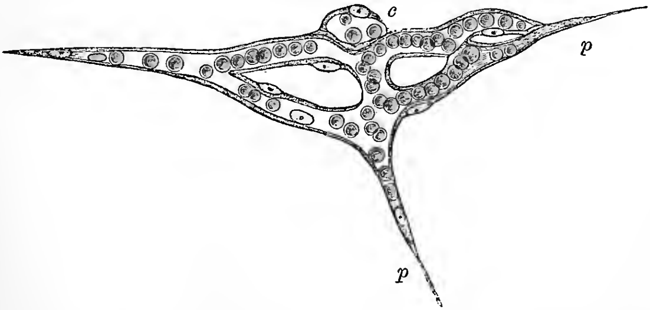


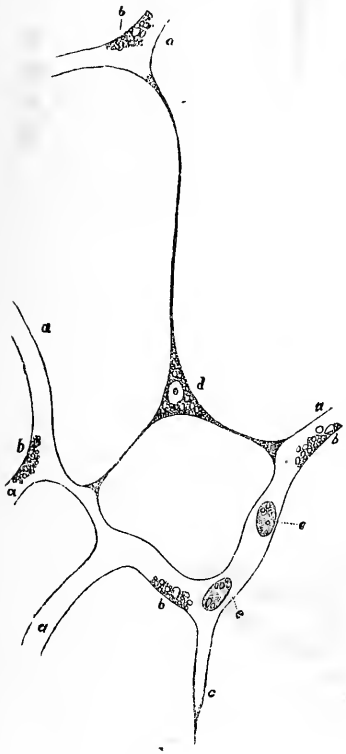
Fig. 195.—Isolated capillary network formed by the junction of several hollowed-out cells, and containing coloured blood-corpuscles in a clear fluid.

c, a hollow cell the cavity of which does not yet communicate with the network ; *p*, *p*, pointed cell-processes, extending in different directions for union with neighbouring capillaries.

extends through the cell processes into those of neighbouring cells and into those sent out from pre-existing capillaries (fig. 194, *bl*), but a more or less extensive capillary network is often formed long before the connection with the rest of the vascular system is established (fig. 195). Young capillaries do not exhibit the well-known lines when treated with nitrate of silver, for the differentiation of the hollowed cells and cell-processes into flattened cellular elements is usually a subsequent process.

The mode of extension of the vascular system in growing parts of older animals, as well as in morbid new formations, is quite similar to that here described, except that blood-corpuscles are not developed within the cells which are forming the blood-vessels.

Fig. 196.



The process of development of capillary vessels has long been studied in the tadpole's tail, and is represented in the adjoining figure (fig. 196) by Kölliker, in which the processes of a stellate cell are seen to meet and join with similar pointed processes which shoot out from the sides of neighbouring capillary vessels, and in this manner the new vessels are adopted into the existing system. The junctions of the cells with each other or with capillary vessels are, at first, of great tenuity, and contrast strongly with the central and wider parts of the cells; they appear then to be solid, but they afterwards become pervious and gradually widen, blood begins to pass through them, and the capillary network acquires a tolerably uniform calibre. The original vascular network may become closer by the formation of new vessels in its interstices. This is effected by similarly metamorphosed cells, arising in the areolæ and joining at various points with the surrounding vessels, and also simply by pointed offshoots from the existing capillaries stretching across the intervals and meeting from opposite sides, so as when enlarged to form new connecting arches.

Fig. 196.—Capillary blood-vessels in the tail of a tadpole, magnified 350 diameters (Kölliker).

a, capillaries permeable to blood; *b*, accumulations of granules concealing the nuclei of the vascular wall; *c*, hollow prolongation of a capillary, ending in a point; *d*, a branched cell, containing a nucleus and granules, and communicating by three branches with prolongations of capillaries already formed; *e*, blood-corpuscles.

The blood-vessels may be said to increase in size and capacity in proportion to the demands made on their service. Thus, as the uterus enlarges in pregnancy, its vessels become enlarged, and when the main artery of a limb is tied, or otherwise permanently obstructed, collateral branches, originally small and insignificant, augment greatly in size, to afford passage to the increased share of blood which they are required to transmit, and by this adaptation of them to the ex-

gency, the circulation is restored. In such cases, an increase takes place in length, as well as in diameter, and accordingly the vessels very commonly become tortuous.

Recent Literature:—On the structure of blood-vessels in general:—*Eberth* in Stricker's Handbook, 1871 (contains also literature up to that time); *Ranvier* in Traité Technique, 1876.

On the structure of arteries:—*v. Ebner* in Med. Centralbl., 1869 (aorta); *Bresgen* in Virch. Arch., LXV. 1875; *Bardeleben* in Jena Sitzungsb., 1878; *Key-Aberg* (aorta) in Biolog. Unters., herausg. von G. Retzius, 1881.

On the structure of veins:—*Bardeleben* in Jena Sitzungsb., 1877 and 1880.

On the structure of capillaries:—*Auerbach; Eberth; Aeby* in Med. Centralbl., 1865; *Chrzonszczewsky*, Virch. Arch., XXXV. 1865; *Tarchanoff* in Pfluger's Arch., IX. 1874; *Stricker* in Wiener Sitzungsb., 1876, and Med. Jahrb., 1878 (contractility).

On the development of blood-vessels:—*His*, Entwickl. d. Hühnchens, 1868; *Klein*, in Wiener Sitzungsb., LXIII. 1871; *Rouget* in Arch. de Physiol., 1872; *F. M. Balfour* in Quart. Jour. of Micr. Sci., 1872; *Schäfer* in Proc. Roy. Soc., 1873; *Ranvier* in Arch. de Physiol., 1873; *Schmidt* in Monthly Micr. Jour., 1875; *Leboucq* in Bull. d. l. Soc. de Méd. de Gand, 1875, and Recherches, &c., 1876; *Kölliker*, "Entwickelungsgesch.," 1879.

LYMPHATIC SYSTEM.

Under this head we include not only the vessels specially called lymphatics or absorbents, together with the glands belonging to them, but also those named lacteal or chyliferous, which form part of the same system, and differ in no respect from the lymphatics, save that they not only carry lymph like those vessels, but are also employed to take up the chyle from the intestines during the process of digestion and convey it into the blood. An introductory outline of the lymphatic system has already been given at page 33.

A system of lymphatic vessels is superadded to the sanguiferous in all classes of vertebrated animals, but this is not the case in the invertebrata; in many of these, the sanguiferous vessels convey a colourless or nearly colourless blood, but no additional class of vessels is provided for conveying lymph or chyle.

Distribution.—In man and those animals in which they are present, the lymphatic vessels are found in nearly all the textures and organs which receive blood; the exceptions are few, and with the progress of discovery may yet possibly disappear. It is, however, with the connective tissue of the several textures and organs that the lymphatics are most intimately associated; indeed, as we shall immediately have occasion to notice, these vessels may be said to take origin in spaces in that tissue. The larger lymphatic trunks usually accompany the deeply-seated blood-vessels; they convey the lymph from the plexuses or sinuses of origin towards the thoracic duct. The principal lymphatic vessels of a part exceed the veins in number but fall short of them in size; they also anastomose or intercommunicate with each other much more frequently than the veins alongside of which they run.

It not unfrequently happens that a lymphatic vessel or a close interlacement of lymphatic vessels, may ensheath an artery or vein either partially or wholly. In this case the lymphatic is termed "perivascular."

Origin.—Two modes of origin of lymphatic vessels are described, viz., the *plexiform* and the *lacunar* or *interstitial*, but no sharp line of distinction can be drawn between them, the difference depending chiefly upon the nature of the tissue or organ to which the lymphatics are distributed. Thus in flat, membranous or expanded parts, the lymphatic vessels usually form a network which is situated either in a single plane, as in many parts of the serous membranes, or in two or more planes

united by intervening vessels, as in the skin and some mucous membranes. In the latter case the strata are generally composed of finer vessels, and form a closer network, the nearer they are to the surface of

Fig. 197.

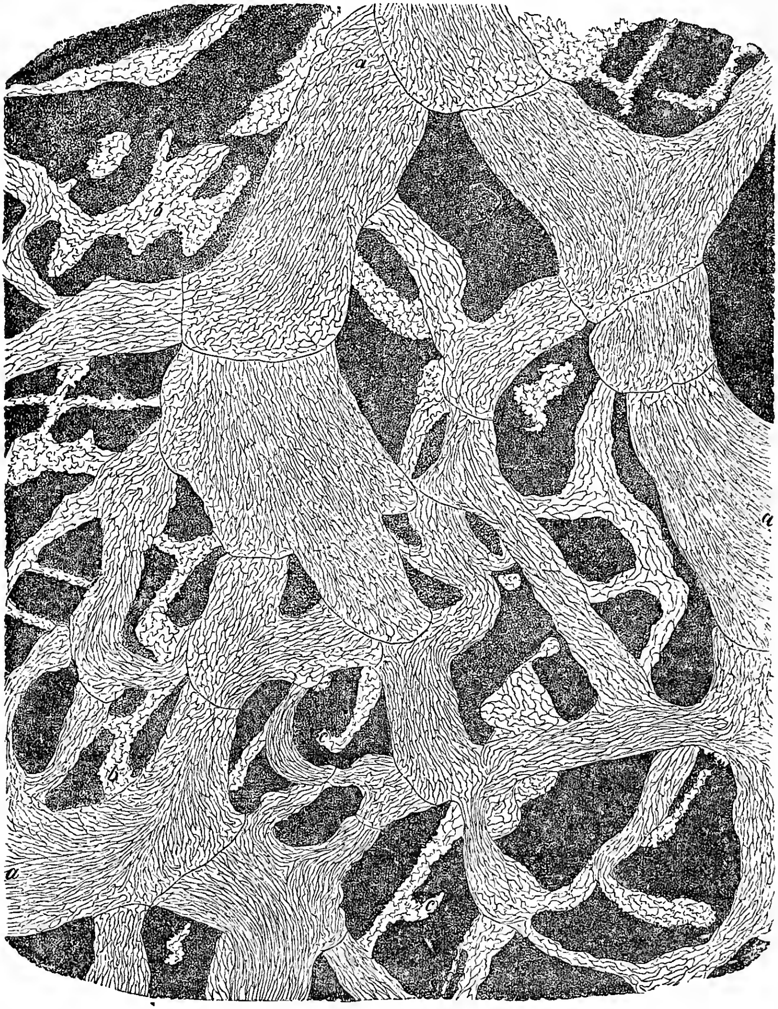


Fig. 197.—LYMPHATIC PLEXUS OF CENTRAL TENDON OF DIAPHRAGM OF RABBIT, PLEURAL SIDE (Klein). MAGNIFIED.

a, larger vessels with lanceolate cells and numerous valves ; *b*, *c*, lymphatics of origin, with wavy-bordered cells. Here and there an isolated patch of similar cells.

the membrane in which they are distributed, but even the most superficial and finest network is composed of vessels which are larger than the sanguiferous capillaries.

The lymphatics of origin are often very irregular in size and shape (fig. 197, *b*, *c*). In them the lymph is collected, and it is conveyed away from the tissues and organs by more regular vessels provided with valves (fig. 197, *a*), which again combine to form larger lymphatic trunks.

Here and there vessels are seen joining the plexuses of origin which arise in the tissue by a blind and often irregular extremity. A long-known and well-marked example of such a mode of commencement is to be found in the lacteals of the intestinal villi, which, although they form networks in the larger and broader villi, arise in others by a single vessel beginning with a blind or closed extremity at the free end of the villus, whence it sinks down to join the general plexus of the intestinal membrane.

On the other hand in the more solid organs the lymphatic vessels occupy the interstices of the organ, and in many cases lose in great measure their character of distinct tubular canals, and appear simply as cleft-like spaces; which are, however, always bounded by an epithelial layer, like that which lines the lymphatic vessels elsewhere.

The lacunar mode of origin of lymphatics was first described in the testis by Ludwig and Tomsa, and it is now known to be characteristic of most glandular organs. Occupying everywhere the interstices of the penetrating connective tissue, the lymph bathes the exterior of the tubules or alveoli of the gland, in many parts even separating them from the capillary blood-vessels, so that the exchanges of material between the plasma of the blood and the secreting cells of the gland must be carried on through the intermedium of the lymph in these spaces. A network of lymphatic spaces is also met with between the anastomosing muscular fibres of the heart.

What may be regarded as a third mode of origin of lymphatics is to be found in the open communications which subsist between the serous cavities and the lymphatic vessels in their walls. These orifices or *stomata*, which will be described with the serous membranes, allow of the passage of lymph from the serous cavities into the lymphatics, so that those cavities may, in a certain sense, be looked upon as large lymph lacunæ. Owing to this communication fluid is not, under normal circumstances, suffered to accumulate in them.

In some of the lower animals the lacunar condition of lymphatics has been long known. Rusconi found that the aorta and mesenteric arteries of amphibia are inclosed in large lymphatic spaces. Johannes Müller recognised the spaces which so extensively separate the frog's skin from the subjacent muscles as belonging to the lymphatic system, and Recklinghausen has shown that the subcutaneous lymph-spaces of the frog's leg communicate with lymphatic vessels which envelope the blood-vessels of the foot; also that milk injected into these spaces finds its way into the blood. The lymphatic system, in being thus constituted by lacunæ or interstitial receptacles, so far agrees with the sanguiferous system of crustaceans and insects.

Structure.—In structure the larger lymphatic vessels much resemble the veins, only their coats are thinner, so thin and transparent indeed that the contained fluid can be readily seen through them. When lymphatics have passed out from the commencing plexuses and lacunæ, they are found to have three coats. The internal coat is covered with an epithelial lining, consisting of a single layer of flattened nucleated cells, which have mostly an oblong or lanceolate figure, with an indented or bluntly serrated border, by which the adjacent cells fit to each other

(fig. 197, *a*). Outside the epithelial layer the inner coat is formed of a layer or layers of longitudinal elastic fibres. The middle coat consists of plain muscular tissue disposed circularly, mixed with finely reticulating elastic fibres taking the same direction. Over the dilatations which occur in the vessels beyond each of the valves, the circular disposition of the muscular fibres gives place to a more irregular disposition, taking the form of an intricate interlacement of fibres. The external coat is composed mainly of white connective tissue with a sparing intermixture of longitudinal elastic fibres, and some longitudinal and oblique bundles of plain muscular tissue. In the thoracic duct there is a subepithelial layer (as in the arteries); and in the middle coat there is a longitudinal layer of white connective tissue with elastic fibres, immediately within the muscular layer. The muscular fibres of the middle coat, although for the most part transverse in direction, are nevertheless many of them oblique or even longitudinal.

The larger lymphatics have bloodvessels ramifying in their outer coat.

The commencing lymphatics or lymphatic capillaries, whether in plexuses or single (as in the villi), have a much simpler structure, their wall being entirely formed of a layer of flattened epithelial cells either similar in form to those lining the larger vessels or (more frequently) presenting a characteristic waved border like the epidermic cells of grasses and some other plants (fig. 198).

Fig. 198.

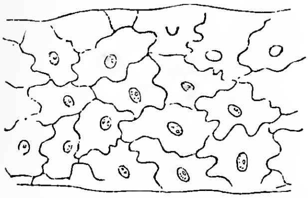


Fig. 198.—Epithelium of commencing lymphatic (Auerbach). 240 diameters.

Gaskell describes an attachment of elastic fibres to the walls of the smaller lymphatics in some parts, and infers that the patency of the lumen of these vessels may by this means be restored after it has been temporarily obliterated by pressure.

Valves.—The lymphatic and lacteal vessels are furnished with valves serving the same office as those of the veins, and for the most part constructed after the same fashion. They generally consist of two semilunar folds arranged in the same way as in the valves of veins already described, but deviations from the usual structure here and there occur. A difference is found in the epithelium upon the two surfaces of the valves similar to that which has been noticed in the valves of the veins.

Valves are not present in all lymphatics, but where they exist they follow one another at much shorter intervals than those of the veins, and give to the lymphatics, when much distended, a beaded or jointed appearance. Valves are placed at the entrance of the lymphatic trunks into the great veins of the neck. They are generally wanting in the reticularly arranged vessels which compose the plexuses of origin already spoken of; so that fluid injected into one of these vessels runs in all directions, so as to fill a greater or a less extent of the plexus, and passes along the separate vessels which issue from it.

The lymphatics of fishes and amphibia are, generally speaking, destitute of valves, and may therefore be injected from the trunks; in the turtle a few valves are seen on the larger lacteals which pass along the mesentery, but none on those in the coats of the intestine; and valves are

much less numerous in the lymphatics and lacteals of birds than in those of mammiferous animals.

Relation of the lymphatics of origin to the cells and cell-spaces of the connective tissue.—It has been already stated (p. 58) that the cells of the connective tissue lie in spaces in the ground-substance which they more or less completely fill. These cells and cell-spaces form in many parts an intercommunicating network of varying fineness extending throughout the substance of the tissue (fig. 199, *d*, *d*,

Fig. 199.

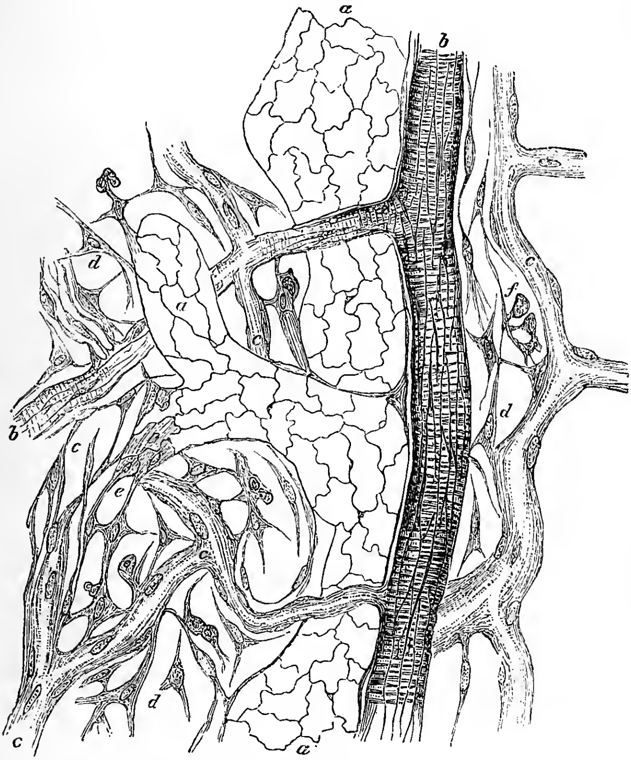


Fig. 199.—Nitrate of silver preparation from rabbit's omentum (Klein). Magnified.

a, lymphatic vessel ; *b*, artery ; *c*, capillaries ; *d*, branched cells of the tissue which are seen to be connected both with the capillary walls, and, as at *e*, with the lymphatic.

fig. 200, *c*, *c*), whilst in other parts the cells acquire a broad flattened form, and joining edge to edge with other similar cells may in this way form an epithelioid patch in the ground substance. Not unfrequently the cells in such a patch take on the wavy border described above as met with in the lymphatics of origin (see the isolated patches in fig. 197). Further, the flattened cells which form the walls of the lymphatics are connected here and there both with the more ramified cells of the tissue (fig. 199, *e*) and with those which form

the epithelioid patches, and in silvered preparations they appear to be continuous with one another. The epithelioid patches look in fact like a part of the lymphatic vessels, and are commonly regarded as such: it must be understood, however, that the spaces here spoken of, whether containing single cells or groups, are not true *vessels*, but merely vacui-

Fig. 200.

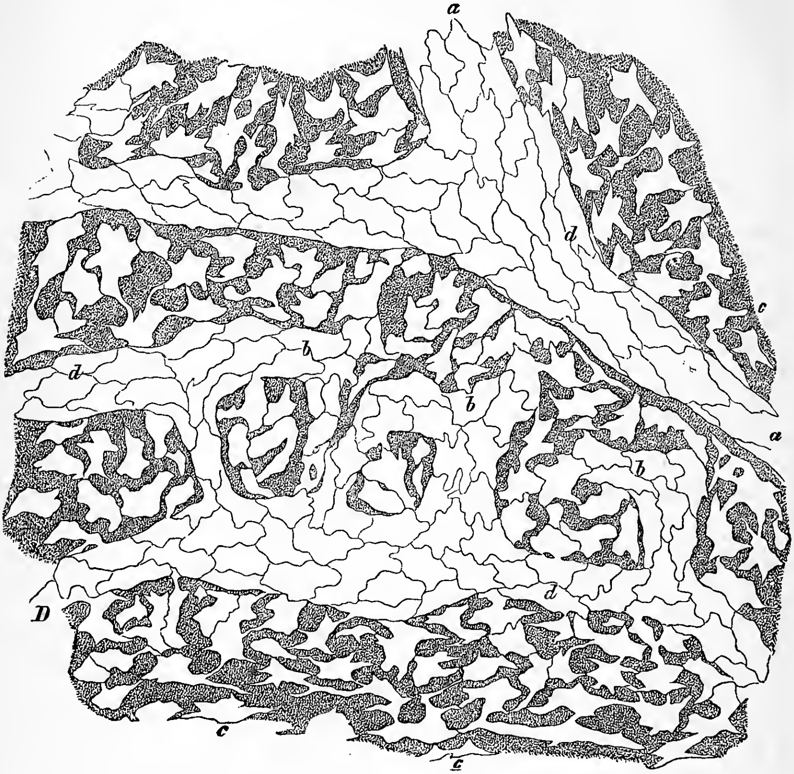


Fig. 200.—Portion of serous membrane of diaphragm (pleural) from the rabbit, treated with nitrate of silver after removal of superficial epithelial layer (Recklinghausen).

c, c, cell-spaces of tissue; *d, d,* commencing lymphatic vessels connected at *b, b,* with the cell-spaces.

ties in the ground-substance of the tissue containing flattened cells, which do not form a continuous vascular wall. And although the spaces present a very close relation to the lymphatic vessels, they can hardly be considered as actually opening into them by patent orifices, for the lymphatics proper have a complete wall of flattened cells united by a small amount of intercellular substance: at the same time this thin film can offer but a very slight resistance to the passage of fluid from the tissue into the vessel, or even to the passage of leucocytes or migrating cells, which, as is well known, penetrate the at least equally closed wall of the blood-vessels.

It has been a question whether the cell-spaces of the connective tissue are in every case and completely filled by the cells, or whether the spaces may in some cases be either devoid of cells altogether, or but partially occupied by them; so that room is left for the free passage of fluid. On this point we would remark that in many cases it is impossible to observe a difference between the forms of the *cells* as shown by the gold method, and those of the *spaces* as shown by treatment with nitrate of silver, so that in these instances, at least, no open lymph-passage can be said to exist; but in other cases the spaces are relatively larger, and here, no doubt, the part unoccupied by the contained cell may be filled by fluid. In œdematous conditions of the tissue, the cell-spaces become somewhat distended with serous fluid, and then in all cases they appear distinctly larger than the cells. Even where the *Saft-canälchen* or lymphatic canaliculi (which correspond with the cell-spaces) are completely filled by protoplasmic cells, lymph can still readily find its way between the cells and the ground-substance by which they are closely surrounded. In other cases where the cells incompletely fill the cavities, a freer passage is left for both fluid and migratory corpuscles.

A point still more difficult to decide is the existence or not of an open communication between the areolæ of the connective tissue and the lymphatic vessels. The result of the injection of coloured fluids into the meshes of the areolar tissue in many parts would lead to the conclusion that some such communication may really exist, for the injection most generally finds its way into the lymphatics. But it is very difficult to demonstrate such a connection anatomically, and up to the present time it can scarcely be said to be proved. It must be remembered that the ground-substance of the connective tissues is itself by no means impermeable to fluids, nor as we have just stated can it be supposed that the delicate walls of the commencing lymphatics can oppose any material obstacle to the passage of fluid into their cavity.

Terminations of lymphatics.—The absorbent system discharges its contents into the veins at two points, namely, at the junction of the subclavian and internal jugular veins of the left side by the thoracic duct, and at the corresponding part of the veins of the right side by the right lymphatic trunk. The openings, as already remarked, are guarded by valves. It sometimes happens that the thoracic duct divides, near its termination, into two or three short branches, which open separately, but near each other; more rarely, a branch opens to the vena azygos—indeed the main vessel has been seen terminating in that vein. Again it is not uncommon for larger branches, which usually join the thoracic duct, to open independently in the vicinity of the main termination; and this is more apt to happen with the branches which usually unite to form the right lymphatic trunk. By such variations the terminations in the great veins are multiplied, but still they are confined in man to the region of the neck; in birds, reptiles, and fishes, on the other hand, communications take place between the lymphatics of the pelvis, posterior extremities and tail, and the sciatic or other considerable veins of the abdomen or pelvis.

The alleged terminations of lymphatics in various veins of the abdomen, described by Lippi as occurring in man and mammalia, have not been met with by those who have since been most engaged in the prosecution of this department of anatomical research, and accordingly his observations have generally been either rejected as erroneous, or held to refer to deviations from the normal condition. Nuhn, of Heidelberg, affirmed the regular existence of these abdominal terminations, and referred to three instances which he met with himself. In two of these the lymphatics opened into the renal veins, and in the other into the vena cava.

Lymphatic hearts.—J. Müller and Panizza, nearly about the same time, but independently of each other, discovered that the lymphatic system of reptiles is furnished, at its principal terminations in the venous system, with pulsatile muscular sacs, which serve to discharge the lymph into the veins. These organs, which are named lymph-hearts, have now been found in all the different orders of reptiles. In frogs and toads two pairs have been discovered, a posterior pair, situated in the sciatic region, which pour their lymph into a branch of the sciatic or of some other neighbouring vein, and an anterior more deeply-seated pair, placed over the transverse process of the third vertebra, and opening into a branch of the jugular vein. The parietes of these sacs are thin and transparent, but contain muscular tissue, which here and there appears obscurely striated, decussating in different layers, as in the blood-heart. In their pulsations they are quite independent of the latter organ, and are not even synchronous with each other. In salamanders, lizards, serpents, tortoises, and turtles, only a posterior pair have been discovered, which, however, agree in all essential points with those of the frog. In the goose, and in other species of birds belonging to different orders, Panizza discovered a pair of lymph-sacs opening into the sacral veins, and Stannius has since found that these sacs have striated muscular fibres in their parietes. Nerve-fibres, both dark-bordered and pale, have been observed in the lymph-hearts of the frog, and also nerve-cells in those of the common tortoise (Waldeyer).*

Development of lymphatic vessels.—The development of lymphatic capillaries has been studied by Klein in the serous membranes. He finds that the process is similar to that of the development of blood-vessels. A vacuole is formed with in one of the cells of the connective tissue, and becomes gradually larger, so as ultimately to produce a cavity filled with fluid, with the protoplasm of the cell thinned out to form the wall of the vesicle thus produced. From this protoplasmic wall portions bud inwards into the cavity, eventually becoming detached as lymph-corpuscles. Meanwhile the nucleus of the cell has become multiplied, and the resulting nuclei are regularly arranged in the protoplasmic wall, which now exhibits, on treatment with nitrate of silver, the well-known wavy epithelial marking characteristic of the lymphatic capillaries. To form vessels, the vesicles become connected with one another by means of processes into which their cavities extend.

The cells lining these lymphatic vesicles, which are common in the mesogastrium of the frog and toad in the winter season bear, in the female of those animals, cilia directed inwards towards the cavity of the vesicles. As the development into vessels proceeds, the cilia disappear (Klein). Remak, who first noticed these ciliated vesicles, took them for cysts in the membrane.

Kölliker has observed the formation of lymphatics from ramified cells in the tails of young salamander-larvæ. He states that the process takes place nearly in the same manner as in the case of sanguiferous capillaries ; the only notable difference being, that whilst the growing lymphatics join ramified cells, and thus extend themselves, their branches very rarely anastomose or become connected by communicating arches.

LYMPHATIC GLANDS.

Lymphatic glands, named also *conglobate glands*, and by modern French writers *lymphatic ganglions*, are small solid bodies placed in the

* Müller's description is to be found in the Philosophical Transactions for 1833; Panizza's in a special memoir on the Lymphatic System of Reptiles, published in the same year. For a more complete account of the lymphatic hearts the reader is referred to the "Leçons d'Anatomie Générale," delivered by Prof. Ranvier in the Collège de France in 1877–78, and published in 1880. A paper on the same subject by Mr. J. Priestley in the Journal of Physiology, Vol. I. 1878, may also be consulted.

course of the lymphatics and lacteals, through which the contents of these vessels have to pass in their progress towards the thoracic or the right lymphatic duct. These bodies are collected in numbers alongside of the great vessels of the neck, and also in the thorax and abdomen, especially in the mesentery and alongside of the aorta, vena cava inferior, and iliac vessels. A few, usually of small size, are found on the external parts of the head, and considerable groups are situated in the axilla and groin. Some three or four lie on the popliteal vessels, and usually one is placed a little below the knee, but none farther down. In the arm they are found as low as the elbow joint.

The lymph of some lymphatic vessels has to traverse two, three, or even more lymphatic glands before reaching the thoracic duct, whilst, on the other hand, there are lymphatics which enter the thoracic duct without having traversed any gland in their way.

The size of lymphatic glands is very various, some being not much larger than a hempseed, and others as large as an almond or a kidney

Fig. 201.

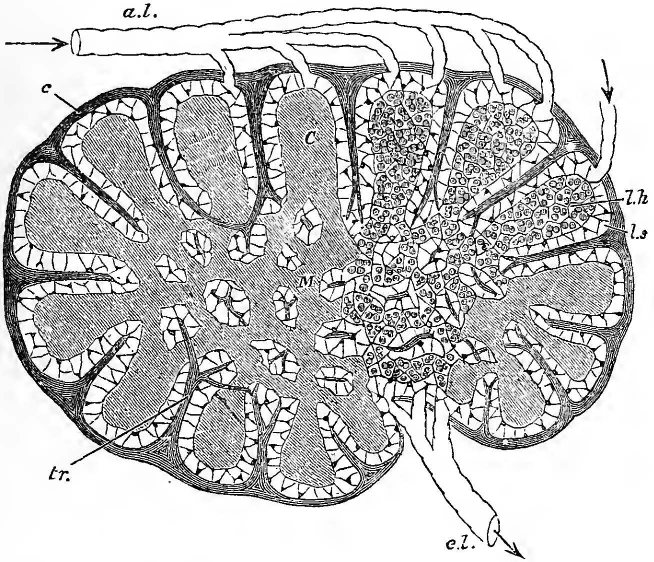


Fig. 201.—DIAGRAMMATIC SECTION OF LYMPHATIC GLAND (Sharpey).

a. l, afferent; *e. l*, efferent lymphatics. C, cortical substance. M, reticulating cords of medullary substance. *l. s*, lymph-sinus; *c*, fibrous coat sending trabeculæ, *tr*, into the substance of the gland.

bean, or even larger than this. In shape, too, they present differences, but most of them are round or oval.

The lymphatics or lacteals which enter a gland are named inferent or afferent vessels (*vasa inferentia* seu *afferentia*), and those which issue from it efferent vessels (*vasa efferentia*). The afferent vessels (fig. 201, *a. l*), on approaching a gland, divide into many small branches, which enter the gland; the efferent vessels commonly leave the gland in the form of small branches, and at a little distance beyond it, or sometimes even

before issuing from it, unite into one or more trunks (*e. l*), usually larger in size but fewer in number than those of the afferent vessels.

A lymphatic gland is covered externally with a coat (figs. 201, 203, *c*) composed of connective tissue, mixed, in certain animals, with muscular fibre-cells. This coat or capsule dips into the interior of the gland at the place where the larger blood-vessels and the efferent lymphatics pass into and out of the organ ; and this part of the gland, which often presents a depression or fissure, is named the *hilus* (fig. 202, *a*). The proper substance of the gland consists of two parts, the *cortical* (fig. 201, *C*), and within this the *medullary* (*M*). The cortex occupies all the superficial part of the gland, except the hilus, and in the larger glands may attain a thickness of one or two millimeters. The medullary portion occupies the centre and extends to the surface at the hilus. It is most developed in the inwardly-seated glands, such as the lumbar and mesenteric, whilst in the subcutaneous glands it is more encroached upon by the connective tissue which enters with the larger

Fig. 202.

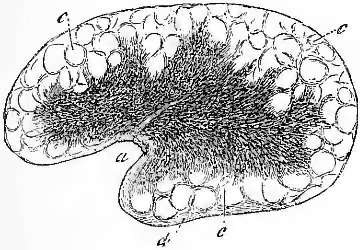


Fig. 202.—Section of a mesenteric gland from the ox, slightly magnified (Kölliker).

a, hilus ; *b*, medullary substance ; *c*, cortical substance with indistinct alveoli ; *d*, capsule.

Fig. 203.

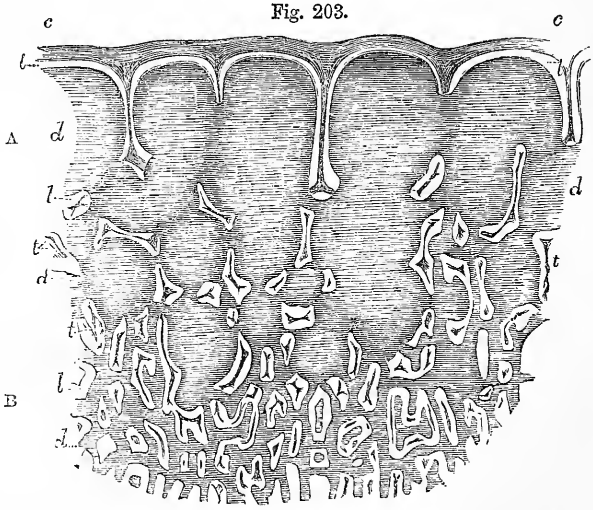


Fig. 203.—Section of a mesenteric gland of the ox (magnified 12 diameters). After His.

The section includes a portion of the cortical part, A, in its whole depth, and a smaller portion of the adjoining medullary part, B ; *c*, *c*, outer coat or capsule sending partitions into the cortical part, eventually forming the trabeculæ, *t*, *t*, which are seen mostly cut across ; *d*, *d*, the glandular substance forming nodules in the cortical part, A, and reticulating cords in the medullary part, B ; *l*, *l*, lymph-sinus or lymph-channel, left white.

blood-vessels at the hilus, and surrounds them, together with the lymph-vessels, in the centre of the gland, so that in these the medullary part is reduced to a layer of no great thickness bounding inwardly the cortical part.

Throughout both its cortical and medullary part the gland is pervaded by a trabecular frame-work which incloses and supports the proper glandular substance. The trabeculæ pass inwards from the capsule (fig. 203). They consist, in the ox and most animals, chiefly of plain muscular tissue; in man, of connective tissue, sparingly intermixed with muscular fibre-cells. In the cortical part they are mostly lamellar in form, and divide the space into small compartments, *alveoli*, from $\frac{1}{60}$ to $\frac{1}{24}$ of an inch wide, which communicate laterally with each other through openings in the imperfect partitions between them (fig. 203, A). On reaching the medullary part the trabeculæ take the form of flattened bands or cords, and by their conjunction and reticulation form a freely intercommunicating meshwork throughout the interior. (In the figure they are represented mostly as cut across.) In these alveoles and meshes is included the proper *glandular substance*, which appears as a tolerably firm pulp or parenchyma, agreeing in nature with lymphoid tissue. Within the alveoli of the cortical part this forms rounded nodules (fig. 203, A, *d*); in the trabecular meshes of the medullary part it takes the shape of rounded cords (*lymphoid cords*) joining in a corresponding network (fig. 203, B, *d*); and, as the containing meshes inter-communicate, so the contained gland-pulp is continuous throughout. But both in the cortical alveoles and the medullary trabecular meshes, a narrow space, left white in the figs. (fig. 201, *l. s*; 203, *l*, *l*) is left all round the gland-pulp, between it and the alveolar partitions and trabecular bands, like what would be left had the pulp shrunk away from the inside of a mould in which it had been cast. This space is both a receptacle and a channel of passage for the lymph that goes through the gland; it is named the *lymph-sinus*, or *lymph-channel*. It is traversed by retiform connective tissue (figs. 204, *a*; 205, *c*, *c*), in which the nuclei of the ramified cells are mostly apparent, and is filled with fluid lymph, containing many lymph-corpuscles, which may be washed out from sections of the gland, so as to show the sinus, while the firmer gland-pulp, which the sinus surrounds, keeps its place. The proper glandular substance is also pervaded and supported by small but fine retiform tissue, mostly non-nucleated (figs. 204, *b*, 205, *a*), communicating with that of the surrounding lymph-sinus, but marked off from it by somewhat closer

Fig. 204.

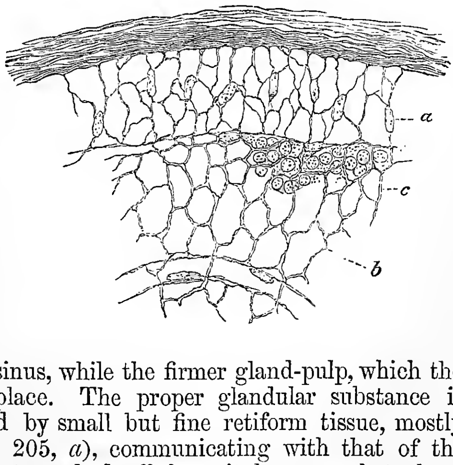


Fig. 204.—THIN SECTION FROM THE CORTICAL PART OF A LYMPHATIC GLAND, MAGNIFIED. (His.)

a, *b*, network of fine trabeculæ formed by retiform or adenoid tissue, from the meshes of which the lymph-corpuscles have been washed out, except at *c*, where they are left.

reticulation at their mutual boundary, not so close, however, as to prevent fluids, or even corpuscles, from passing from the one to the other. The gland-pulp is made up of densely packed lymphoid cells, occupying the interstices of its supporting retiform tissue, and is traversed by an abundant network of capillary blood-vessels (*d*, *d*), which run throughout the proper glandular pulp, both cortical and medullary, but do not pass into the surrounding lymph-sinus. The lymphoid cells of the glandular pulp are similar in their general appearance to white blood- or lymph-corpuscles, except that their nucleus is relatively larger, and their protoplasm much smaller in amount.

Fig. 205.

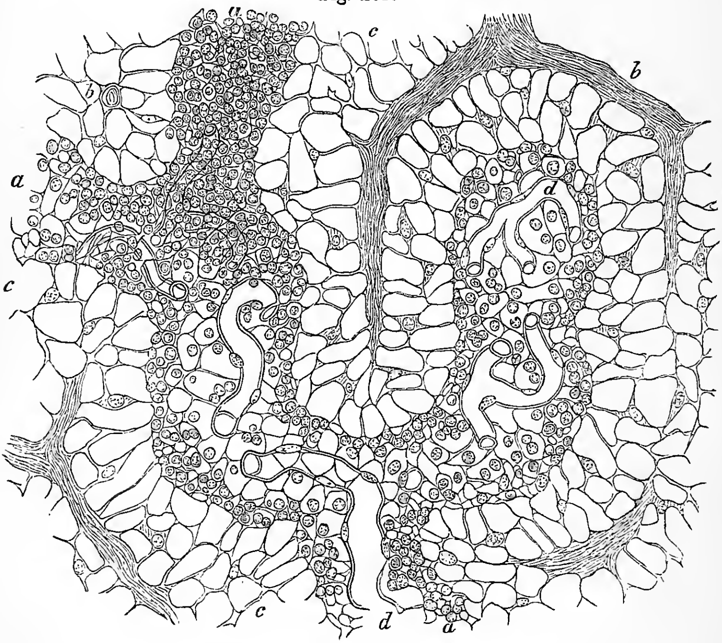


Fig. 205.—Section of the medullary substance of a lymphatic gland (ox). 300 diameters. (Recklinghausen.)

a, *a*, *a*, follicular or lymphoid cords; *c*, lymph-sinus; *b*, *b*, trabeculæ; *d*, *d*, blood-vessels.

The ramified cells of the retiform tissue of the lymph-sinus, which often contain a considerable number of pigment-granules, enclose fine anastomosing bundles of connective tissue fibrils which are continued from the trabeculæ and from the capsule across the lymph-channel (Bizzozero), and pervade the whole of the glandular pulp with a fine network. The trabeculæ themselves have a covering of flattened cells, which on the side turned towards the lymph-channel are provided with processes to anastomose with those of the retiform tissue. The inner surface of the capsule is also lined with flattened cells, which are continuous at the entrance and exit of the lymphatics with the epithelium of those vessels.

According to Bizzozero there is also a complete layer of flattened cells to the glandular pulp.

Arteries enter and veins leave the gland at the hilus, surrounded, in some glands, as already said, with a dense investment of connective tissue. The arterial branches go in part directly to the glandular substance, but partly run along the trabeculæ. The former end in the glandular capillary network above-mentioned, from which the veins begin, and tend to the hilus alongside the arteries. The branches which run along the trabeculæ are partly conducted to the coat of the gland to be there distributed; but most of their branches pass to the glandular substance, the connective tissue of the trabeculæ which ensheaths them passing gradually into the lymphoid tissue of the pulp, so that this at first appears as a sheath to the arterial branch (as in the spleen). The latter soon however breaks up into capillaries which ramify in the gland-pulp, supported by its pervading retiform tissue, which forms an additional adventitious coat around the minute vessels.

As to the lymphatics of the gland, the afferent vessels, after branching out upon and in the tissue of the capsule, send their branches through it to open into the lymph-sinuses of the cortical alveoli, and the efferent lymphatics begin by fine branches leading from the lymph-sinuses of the medullary part, and forming at the hilus a dense plexus of tortuous and varicose-looking vessels, from which branches proceed to join the larger efferent trunks. The lymph-sinus, therefore, forms a channel for the passage of the lymph, interposed between the afferent and efferent lymphatics, communicating with both, and maintaining the continuity of the lymph-stream. The afferent and efferent vessels, where they open into the lymph-sinus, lay aside all their coats, except the epithelial lining, which is continued over the trabeculæ and the interior of the capsule.

It is not unreasonable to presume that, in the proper glandular substance, there is a continual production of lymph-corpuscles, which pass into the lymph-sinus, and that fresh corpuscles are thus added to the lymph as it traverses the gland. This view is supported by the fact, that the corpuscles are found to be more abundant in the lymph or chyle after it has passed through the glands.

Other organs composed of lymphoid tissue.—Bodies which are so far similar in structure to lymphatic glands that they are composed of a retiform tissue, the interstices of which are closely packed with lymphoid cells, and are in intimate relation with the lymphatic vessels of the part, occur in many places. Thus, in the serous membranes, rounded nodules are here and there met with, which, as Klein has shown, are developed either around or at one side of an enlarged lymphatic (perilymphangial nodule, fig. 206, A), or in some cases even within the vessel (endolymphangial nodule, fig. 206, B). The retiform tissue which constitutes the framework of the nodule is connected with the flat cells forming the wall of the lymphatic, and lymphoid cells accumulate in the interstices of the retiform tissue.

The endolymphangial nodules, although small and simple in structure, closely recall the structure of one of the cortical nodules of a lymphatic gland; for a path or channel for the passage of lymph is left between the central accumulation of lymphoid tissue and the wall of the vessel, this path being bridged across by branched cells of the retiform tissue; and along it the lymph must pass very slowly, and come into intimate relation with the tissue of the nodule. In other cases the lymphoid tissue of the serous membranes is less circumscribed, occurring in the form of ill-defined patches or elongated tracts, which lie along the course of the small arteries and veins, receiving from the latter branches which form a capillary network within the tissue.

In mucous membranes, especially that lining the alimentary canal, conspicuous lymphatic nodules are met with in various parts, and here they have been long known. They occur either singly, as in the so-called solitary glands

of the intestine, or collected into groups as in the agminated glands or patches of Peyer, or into thick masses as in the tonsils. In most of these cases the nodules are spherical or dome-shaped condensations of the lymphoid tissue which occurs largely in the substance of the mucous membrane, on the surface of which they may cause a distinct prominence; they are usually found to be in close relation with the lymphatics of the membrane, being either partially surrounded by a large sinus-like lymphatic, or encircled by a plexus of lymphatic vessels. In the mucous mem-

A Fig. 206 B

Fig. 206.—Developing lymphatic (lymphangial) nodules, from the omentum of a guinea-pig (Klein).

A, Perilymphatic nodule; *a*, lymphatic vessel; *c*, part of its epithelial wall, seen in optical section; *e*, lymph-corpuscles within the vessel; *b*, lymphoid tissue of the nodule; *d*, blood-capillaries. B, Endolymphatic nodule; *a*, vein; *b*, artery; *c*, capillaries; *d*, a lymphatic vessel, in which this whole system of blood-vessels is inclosed; *e*, lymphoid tissue within the lymphatic vessel; *f*, wall of the lymphatic in optical section.

brane of the bronchial tubes nodules are met with which are quite similar to those of the serous membranes. In the spleen, tracts of lymphoid tissue, with lymphatics in connexion with them, ensheath the smaller arteries and are dilated at certain points into distinct nodules which have here long been known as the Malpighian corpuscles of the spleen. Lastly the thymus gland seems to be chiefly composed in the young subject of a collection of lymphoid tissue, although in the adult it is usually found to have become transformed into adipose tissue.

The further description of these lymphoid structures, will be deferred until the several organs where they occur are systematically treated of

SEROUS MEMBRANES.

The serous membranes are so named from the apparent nature of the fluid with which their surface is moistened. They lie in cavities of the body which have no obvious outlet, and the chief examples of them are, the peritoneum, the largest of all, lining the cavity of the abdomen; the two pleuræ and the pericardium in the chest; and the tunica vaginalis surrounding each of the testicles within the scrotum.

The arachnoid membrane, which is a delicate connective-tissue membrane surrounding the brain and spinal marrow in the bony cavities in which they are

contained, was formerly reckoned amongst the serous membranes; but neither in the details of its structure, in its general disposition, nor in its development does it correspond with the other serous membranes. It is, therefore, no longer classed with them, but will be described with the other membranes investing the brain and spinal cord.

Form and arrangement.—In all cases a serous membrane has the form of a closed sac, one part of which is applied to the walls of the cavity which it lines, the *parietal* portion; whilst the other is reflected over the surface of the organ or organs contained in the cavity, and is therefore named the *reflected* or *visceral* portion of the membrane. Hence the viscera in such cavities are not contained within the sac of the serous membrane, but are really placed behind or outside of it; seeming to push inwards the part of the membrane which immediately covers them, some organs receiving in this way a complete, and others only a partial and sometimes very scanty investment.

In passing from one part to another, the membrane frequently forms folds which in general receive the appellation of ligaments, as, for example, the folds of peritoneum passing between the liver and the parietes of the abdomen, but which are sometimes designated by special names, as in the instances of the mesentery, mesocolon, and omentum.

The peritoneum in the female sex, is an exception to the rule that serous membranes are perfectly closed sacs, inasmuch as it has two openings by which the Fallopian tubes communicate with its cavity.

A serous membrane sometimes lines a fibrous membrane, as where the serous layer of the pericardium adheres to its outer or fibrous part. Such a combination is often named a *fibro-serous* membrane.

The inner surface of a serous membrane is free, smooth, and polished; and, as would occur with an empty bladder, the inner surface of one part of the sac is applied to the corresponding surface of some other part; a small quantity of fluid, usually not more than merely moistens the contiguous surfaces, being interposed. The parts situated in a cavity lined by serous membrane, being themselves also covered by it, can thus glide easily against its parietes or upon each other, and their motion is rendered smoother by the lubricating fluid.

The outer surface most commonly adheres to the parts which it lines or covers, the connection being effected by means of areolar tissue, named therefore "subserous," which, when the membrane is detached, gives to its outer and previously adherent surface a flocculent aspect. The degree of firmness of the connection is very various: in some parts the membrane can scarcely be separated; in others, its attachment is so lax as to permit easy displacement.

Structure and properties.—Serous membranes are thin and transparent, so that the colour of subjacent parts shines through them. They are tolerably strong, with a moderate degree of extensibility and elasticity. They are lined on the inner surface by a simple epithelial layer of flattened cells (fig. 207), each of which contains a round or oval nucleus with one or two nucleoli, and sometimes an intranuclear network. The cells have, according to Klein, a comparatively coarse network of minute fibrils embedded in the otherwise clear cell-substance. The outlines of the cells may readily be brought into view by treatment with nitrate of silver. The lines of junction of the cells which are thus made evident, may be straight and even, but are most commonly slightly jagged or

sinuous. Here and there between the cells apertures are to be seen, which are of two kinds. The smaller, which are also the more numerous, are occupied either by an accumulation of the intercellular substance or by processes which are sent up to the surface of the membrane from more deeply lying cells (*pseudostomata*, Klein and Burdon-Sanderson) : the larger ones, on the other hand, are true apertures (*stomata*), which are surrounded by a ring of small cubical cells (fig. 208, *s*, *s′*), and open into a subjacent lymphatic vessel, either directly or by the medium of a short canal lined with similar cells. The surface

Fig. 207.

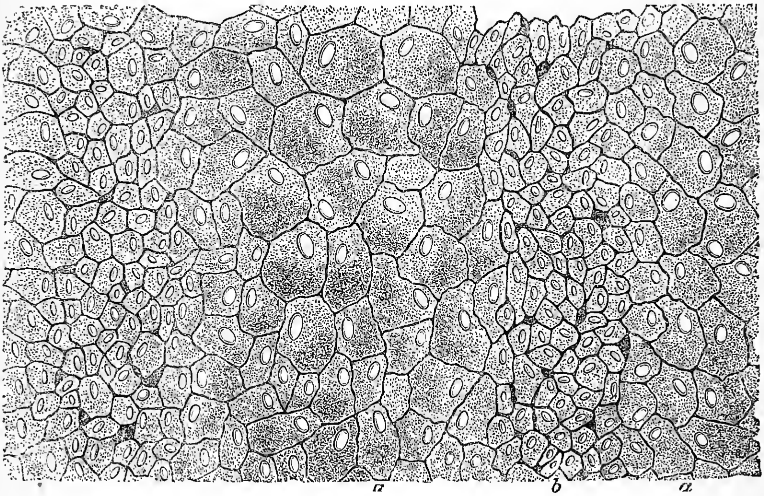


Fig. 207.—Portion of epithelium of peritoneum from diaphragm of rabbit (Klein).

a, larger cells. *b*, smaller ones, with here and there a pseudostoma between.

cells of the serous membrane are not everywhere uniform in size (fig. 207), but patches are here and there met with in which they are smaller and more granular in appearance and it is in these parts that the stomata and pseudo-stomata are more frequently seen. The epithelium-cells of the membrane often present a somewhat radiated aspect near the stomata, the silver lines converging towards the orifice. According to Klein, it is not unfrequent to find evidences of proliferation, especially in the neighbourhood of the stomata and pseudostomata, cells being met with containing two or even many nuclei, and others which are being budded off from the epithelium-cells of the membrane in the form of amœboid lymph-corpuscles.

The stomata were discovered in the peritoneal covering of the central tendon of the diaphragm by Recklinghausen, who found that milk-globules could be made to pass through them into the lymphatics. Similar apertures were found by Ludwig and Dybkowsky in the pleura of mammals, and by Schweigger-Seidel and Dogiel in the septum between the peritoneal cavity of the frog and the great

lymph-sac (cisterna magna) behind it. They have since been discovered on the omentum by Klein, but have not hitherto been shown to exist in the pericardium nor in the tunica vaginalis.

The substance of the membrane underneath the epithelium is composed of a connective tissue ground-substance in which is a variable amount of fibres, both white and elastic; the latter in many serous membranes, as remarked by Henle, are principally collected into a reticular layer near the surface. The bundles of white fibres are also arranged in a reticular manner, frequently uniting with one another,

Fig. 208.

Fig. 208.—Small portion of peritoneal surface of diaphragm of rabbit (Klein). Magnified.

l, lymph-channel below the surface, lying between tendon bundles, *t*, *t*, and over which the surface-cells are seen to be relatively smaller, and to exhibit five stomata, *S*, *S*, leading into the lymphatic. The epithelium of the lymphatic channel is not represented.

and the meshes of the reticulation which they form are occupied by the ground-substance of the membrane, and bridged over by the epithelium-cells of the general surface. In some folds of the serous membranes and especially in the great omentum of many animals, including man, the meshes of the reticulation have become open in many parts owing to the absorption of the intervening ground-substance, so as to allow of a free communication between the two sides of the fold of membrane. In these places the epithelium-cells of the surface are applied to the anastomosing connective tissue bundles, and folded round them so as to bound the apertures between the two surfaces. Where the membrane is thicker, the ground-substance contains bloodvessels and lymphatics, with the lymphoid and adipose tissue which is often found in the serous membranes and especially in their folds; as well as connective tissue corpuscles with their corresponding cell-spaces (figs. 199, 200), which in the serous membranes are very often collected into epithelium-like patches. In parts of the membrane in which the cor-

puscles are more thinly scattered, they possess branching processes, some of which intercommunicate with those of neighbouring cells, others may pass up to the surface of the membrane as pseudostomata and others again, become connected to the walls of the lymphatics and blood-vessels.

In the human subject, the serous membranes appear to be bounded under the epithelium by a distinct basement membrane (Bizzozero).

The **blood-vessels** of the membrane end in a capillary network with comparatively wide meshes, which pervades the subserous tissue and the tissue of the serous membrane. The vessels are much more numerous in the nodules and tracts of lymphoid tissue (see below) as well as in the adipose tissue, which is found largely developed in the serous membranes of fat animals.

The **lymphatics** of the serous membranes are exceedingly abundant. Their relation both to the cell-spaces of the tissue and to the surface of the membrane, as well as their general arrangement, has been already noticed. They are sometimes met with ensheathing the blood-vessels.

Lymphoid tissue.—Nodules of this tissue occur, as before mentioned (p. 213), in the substance of the serous membranes. More generally the lymphoid tissue of the serous membranes takes the shape of elongated tracts which follow the course of the small arteries and veins, receiving from the latter branches which divide to form a capillary network. Lymphatic vessels run in these tracts alongside the blood-vessels, and often partially enclose them. These lymphoid nodules and tracts are more numerous in the young animal; in the adult they are frequently found transformed into lobules and tracts of adipose tissue.

The **nerves** of the serous membranes are destined chiefly for the blood-vessels, and for the most part accompany these in their course. A few pale fibres, however, are distributed to the substance of the membrane, in which they form a plexus with large meshes: from the branches of this plexus, fibrils may be traced which unite into a somewhat finer plexus near the surface.

Recent Literature of the Lymphatic System. On Lymphatic Vessels:—*Recklinghausen,* in Stricker's Handbook, 1871; *J. Arnold,* in Virch. Arch., LXII., 1874; *Foà,* in Virch. Arch., LXV., 1875; *Tarchanoff,* in Arch. de physiol., 1875; *Flemming,* in Arch. f. mikr. Anat., XII., 1876; *Gaskell,* in Arb. d. physiol. Anst. zu Leipzig, 1876; *Dogiel,* in Arch. f. mikr. Anat., XVII., 1879.

On Lymphatic Glands:—*Bizzozero,* in Moleschott's Unters., XII. 1873; *Lodi,* in Riv. clin., 1876.

On Serous Membranes:—*Klein & Burdon Sanderson,* in Med. Centralbl., 1872; *Klein,* in Quart. J. Micr. Sci. XII., 1872 (ciliated vesicles in frog's perit.); "The Serous Membranes," 1873; and in Qu. J. Micr. Sci., 1877 (on the omentum); *Bizzozero,* in Med. Centralbl., 1874; (with *Salvioli*) in Arch. p. le sci. med., 1876, and 1877.

SYNOVIAL MEMBRANES.

These are connective tissue membranes which are found surrounding closed cavities in connection with moveable structures in certain parts, such as the joints, the elongated sheaths in which some tendons glide, and at various situations between the skin and bony prominences below it. Although they resemble serous membranes in some respects, the synovial membranes are distinguished by the nature of their secretion,

which is a viscid glairy fluid resembling the white of an egg, named *synovia.* From its nature it is well adapted for diminishing friction, and thereby facilitating motion.

If a drop of synovial fluid be examined microscopically, it is found to contain (in addition to fat-molecules) a few amœboid corpuscles, as well as cells similar to those which occur on the projections of the membrane.

The different synovial membranes of the body are referred to three classes, viz., *articular, vaginal,* and *vesicular,* or *bursal.*

1. Articular synovial membranes, or *Synovial capsules of joints.*—These by their synovial secretion lubricate the cavities of the diarthrodial articulations, that is, those articulations in which the opposed surfaces glide on each other. In these cases the membrane may be readily seen covering internally the surface of the capsular and other ligaments which bound the cavity of the joint, and affording also an investment to any tendons or ligaments which pass through the articular cavity, as in the instance of the long tendon of the biceps muscle in the shoulder-joint. On approaching the articular cartilages the membrane does not pass over them, but terminates after advancing but a little way on their surface, with which it is here firmly adherent. The synovial membranes, therefore, do not form closed bags lying between the articular cartilages as was supposed by the older anatomists, for the main part of the surfaces of the joints are not covered at all by the membrane, nor even by a layer of epithelium-cells, prolonged from the membrane, as some have described.

In several of the joints, folds of the synovial membrane pass across the cavity; these have been called synovial ligaments. Other processes of the membrane simply project into the cavity at various points. These are very generally cleft into fringes at their free border, upon which their blood-vessels, which are numerous, are densely distributed. The larger folds and processes often contain fat, and then are sufficiently obvious; but many of the folds are small and inconspicuous.

The fringed vascular folds of the synovial membrane were described by Havers in 1691, under the name of the *mucilaginous glands,* and he regarded them as an apparatus for secreting synovia. Rainey found that these *Haversian fringes,* as they are sometimes called, may exist in all kinds of synovial membranes, and that from the primary vascular fringes other smaller secondary processes are sent off, into which no blood-vessels enter.

2. Vaginal synovial membranes or *Synovial sheaths.*—These are intended to facilitate the motion of tendons as they glide in the fibrous sheaths which bind them down against the bones in various situations. The best-marked examples of such fibrous sheaths are to be seen in the hand and foot, and especially on the palmar aspect of the digital phalanges, where they confine the long tendons of the flexor muscles. In such instances one part of the synovial membrane forms a lining to the osseo-fibrous tube in which the tendon runs, and another part affords a close investment to the tendon. The space between these portions of the membrane is lubricated with synovia and crossed obliquely by one or more folds or duplications of the membrane named "fræna," in some parts inclosing a considerable amount of elastic tissue (Marshall).

3. Vesicular or Bursal synovial membranes, *Synovial bursæ, Bursæ mucosæ.*—In these the membrane has the form of a simple sac,

interposed, so as to prevent friction, between two surfaces which move upon each other. The synovial sac in such cases is flattened and has its two opposite sides in apposition by their inner surface, which is free and lubricated with synovia, whilst the outer surface is attached by areolar tissue to the moving parts between which the sac is placed.

In regard to situation, the bursæ may be either deep-seated or subcutaneous. The former are for the most part placed between a muscle or its tendon and a bone or the exterior of a joint, less commonly between two muscles or tendons: certain of the bursæ situated in the neighbourhood of joints not unfrequently open into them. The subcutaneous bursæ lie immediately under the skin, and are found in various regions of the body interposed between the skin and some firm prominence beneath it. The large bursa situated over the patella is a well-known example of this class, but similar though smaller bursæ are found also over the olecranon, the malleoli, the knuckles, and various other prominent parts. It must, however, be observed that, among these subcutaneous bursæ, some are reckoned which do not always present the

Fig. 209.

Fig. 210.

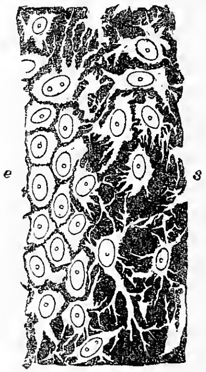


Fig. 209.—Ramified connective-tissue corpuscles, from articular synovial membrane of ox. 250 diameters. (E. A. S.)

Fig. 210.—Portion of the surface of a vaginal synovial membrane, after treatment with nitrate of silver. 250 diameters (E.A.S.).

The cell-spaces of the tissue and the nuclei of the contained cells only are represented. *e*, epithelioid arrangement of cells; *s*, ramified cells.

characters of true synovial sacs, but look more like mere recesses in the subcutaneous areolar tissue, larger and more defined than the neighbouring areolæ, but still not bounded by an evident synovial membrane. These may be looked on as examples of less developed structure, forming a transition between the areolar tissue spaces and perfect synovial cavities.

Structure of synovial membranes.—The synovial membranes are composed entirely of connective tissue with the usual cells and fibres of that tissue. It was formerly stated, and is still asserted by Tillmanns and others, that they are lined with an epithelial layer of flattened cells, similar to those lining the serous membranes, but, as was shown by Hüter, there exists on the synovial membranes no complete lining of the kind. Patches of cells may, it is true, here and there be met with which present an epithelioid appearance (fig. 210, *e*), as, indeed, we know to be the case in the connective tissue of other parts; but most of the surface-cells of the synovial membranes are of the irregularly-branched type (figs. 209, 210, *s*), the surface of the membrane between the cells and sometimes also over them being formed by the ground-substance of the connective tissue, whilst here and there small blood-vessels come close to the surface from subjacent parts. The cells are in many places smaller than in connective tissue generally. They vary much in shape in different parts, sometimes forming a network in the tissue by the anastomoses of their ramifying processes, in other parts being rounded, and more closely arranged.

The cells of the vaginal synovial membrane are often slightly elongated in the direction of the axis of the tendon.

The articular synovial membranes pass, as before said, a certain distance over the cartilages of the joints. They do not, however, end abruptly, but shade off gradually into the margin of the cartilage, the

Fig. 211.

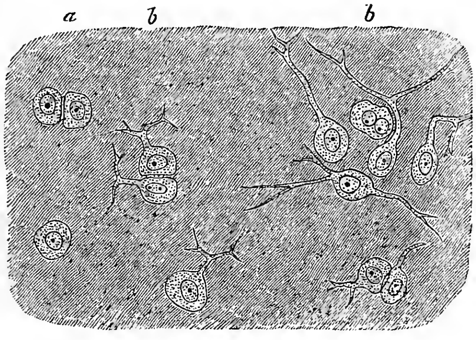


Fig. 211. Transition of cartilage-cells into connective-tissue corpuscles of synovial membrane. About 340 diameters. From head of metatarsal bone, human. (E.A.S.)

a, ordinary cartilage cells; *b*, *b*, with branched processes.

fibrous tissue becoming fibro-cartilage and the cells gradually losing their processes and becoming transformed into cartilage-cells (fig. 211), so that it is difficult to say where the one structure begins and the other ends. This portion of the synovial membrane, or of the cartilage, is known as the "marginal zone;" it is best marked around the convex heads of the bones, and is especially well seen near the lower margin of the patella (Hüter).

The Haversian folds and fringes, at least the larger ones, agree in general structure with the rest of the tissue of the synovial membrane, except that, as before remarked, some of them contain fat; their surface

layer contains for the most part irregularly stellate cells, except over the fat, where there is occasionally to be observed a true epithelioid covering like that of a serous membrane. The smaller non-vascular secondary fringes of Rainey (*synovial villi*) are minute finger-shaped processes projecting from the margins of the larger ones, and consist for the most part of small rounded cells with granular protoplasm and but little intercellular substance, enclosing a central strand of connective-tissue fibrils; and in some cases even one or two cartilage-cells. Some of the synovial villi are entirely made up of fibro-cartilage, being altogether destitute of the covering of rounded cells (Tillmanns).

Vessels and nerves.—The blood-vessels in and immediately beneath the synovial membrane are numerous in most parts of the joints. They advance but a short way upon the cartilages, forming around the margin a vascular zone, named by W. Hunter "circulus articuli vasculosus," in which they end by loops of vessels dilated at the bent part greatly beyond the diameter of ordinary capillaries (Toynbee). In the fœtus these vessels advance further upon the surface of the cartilage than in the adult. The vessels of the vaginal synovial membranes are less numerous than those of the synovial membranes of the joints.

The synovial cavities do not appear to have so close a relation to the lymphatic system as is the case with the serous cavities. For although lymphatic vessels have been described by Tillmanns and others in the synovial membranes, they have not been shown to communicate with the cavities, nor do they as a rule lie near the free surface. In this respect they differ from the blood-capillaries, which may come close up to the inner surface of the membrane.

W. Krause describes the nerves of the synovial membranes (at least those of the joints) as terminating in peculiar corpuscles allied to end-bulbs. Another observer (Nicoladoni) has traced nerves into a plexus of pale fibrils lying close under the surface of the membrane.

Development.—At the time of the formation of a joint by cleavage the tissue around it forms, in its outer part, the fibrous capsule of the joint; in its inner part, the commencement of the synovial membrane. The cartilage cells on the surfaces of the newly formed joint are at first, like those of the embryonic cartilage generally, placed closely together without matrix or intercellular substance; after a time this appears in fine lines between the cells, so that there is then presented, in silvered preparations, an epithelioid appearance. By a further development of intercellular substance the superficial cells become more separated from one another, and now possess an irregularly branched shape with communicating processes. Near the edge of the cartilage this condition is permanent, so that the marginal zone of the synovial membrane is formed *in situ* from what was originally cartilage. Nearer the centre of the articular surface, a further change takes place in the progress of development. The cells lose their processes and acquire the characters of ordinary cartilage cells, whilst the matrix between them becomes increased, and forms also a thin layer covering their surface.

Literature.—*Rainey*, Proc. R. S., 1846; *Hueter*, Virch. Arch., xxxvi.; *Albert*, in Wiener Sitzungsb., 1871; *Reÿher*, The cartilages and synovial membranes of the joints, Journ. of Anat. and Physiol., 1874; *Tillmanns*, Histol. d. Gelenke, Arch. f. mikr. Anat., 1874; Lymphgef. d. Gelenke, ibid. xii., 1876; Hist. d. Synovialhäute, Arch. f. klin. Chir., 1876; *Bentzen*, Devel. of joints, Nord. med. arkiv., 1875; *Sluys* in Niederl. Arch. f. Zool., 1876; *Weichselbaum*, in Wiener Sitzungsb. lxxv., 1877.

SECRETING GLANDS.

The term gland has been applied to various objects, differing widely from each other in nature and office, but the organs the structure of which it is proposed to consider generally in the present chapter, are those devoted to the function of secretion.

The element which plays the most important part in the secretory process is the nucleated cell. A series of these cells, which are usually of a spheroidal, polyhedral, or columnar figure, is spread over the secreting surface, in the form of an epithelium, which generally rests on a membrane, named the basement-membrane, or membrana propria. This membrane, itself extravascular, limits and defines the secreting surface; it supports and connects the secreting cells on one side whilst on the other it is in close proximity to the blood-vessels, and it may very possibly, also, minister in a certain degree to the process of secretion, by

Fig. 212.

A B

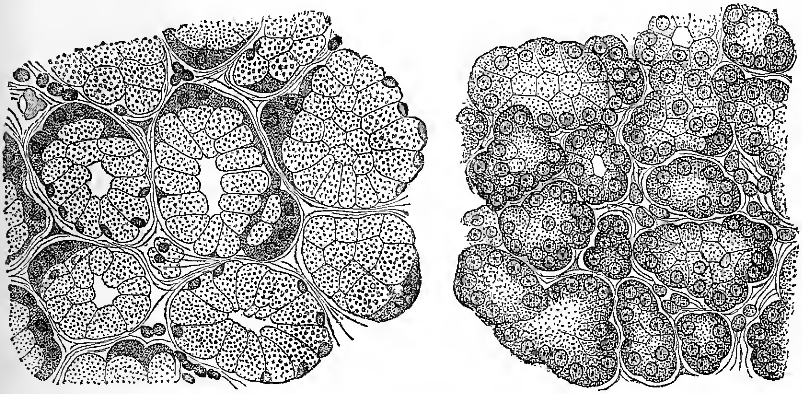


Fig. 212.—Sections of the orbital gland of the dog. A, during rest. B, after a period of activity (Heidenhain after Lavdovsky.)

In A, the cells of the alveoli are large and clear, being filled with the material for secretion (in this case, mucigen) which obscures their protoplasm, but some of the cells have not participated in the formation of the secretion, and these remain small and protoplasmic, forming the crescentic group seen in most of the alveoli.

In B, the accumulated material is discharged from the cells, which appear partially disintegrated in consequence. Both the cells and the alveoli are much smaller, and the protoplasm of all the cells is now apparent.

allowing some constituents of the blood to pass through it more readily than others. But the basement-membrane is not universally present, and it is the cells that are the chief agents in selecting and preparing the special ingredients of the secretions. They attract and imbibe into their interior those substances which, already existing in the blood, require merely to be segregated from the common store and concentrated in the secretion, and they, in certain cases, convert the matters which they have selected into new chemical compounds, or lead them to assume organic structure. A cell thus charged with its selected or converted contents

yields them up to be poured out with the rest of the secretion—the contained substance escaping from it either by exudation or by bursting and destruction of the cell itself. Cells filled with secreted matter may also be detached, and carried out entire with the fluid part of the secretion; and, in all cases, new cells speedily take the place of those which have served their office. The fluid effused from the blood-vessels supplies matter for the nutrition of the secreting structure, besides affording the materials of the secretion.

Changes in the cells during activity.—Since the materials for secretion are selected or prepared by the cells it is not surprising to find that the cells of a secreting gland differ considerably in appearance

Fig. 213.

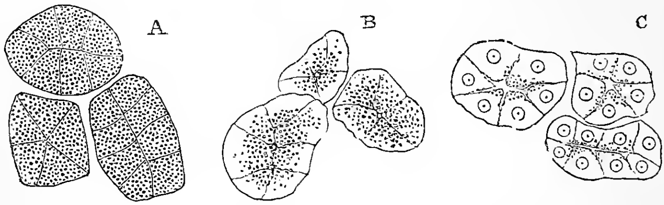


Fig. 213.—Part of a ferment-forming gland; A at rest, B after a short period of activity, C after a prolonged period of activity. (Langley.)

In the resting condition the cells of the gland are almost filled with granules (of zymogen). During activity these become discharged from the cells as ferment, disappearing at first from the outer part of the cell, which is thereby left clear. Finally the granules only remain near the lumen of the alveoli, and near the surfaces of the cells which are contiguous to one another. In A and B the nuclei of the cells are obscured by the granules.

according as the gland is in a condition of rest or activity (fig. 212). In the former case the materials for secretion may have been accumulating within the cells and may be detected within them, whereas in the latter case, if the secretion have been proceeding for some time, the cells may be emptied of the accumulated material, and in many instances may themselves be partially or entirely destroyed, owing to the disruption of their protoplasm in the process of discharge of the secreted matter. In some glands however the accumulation of the materials of secretion within the cells does not go on to any great extent during rest, but begins with the increased activity of the gland consequent on stimulation whether natural or artificial, and proceeds up to a certain point, after which the process of discharge of the accumulated material begins. But according to Heidenhain and Langley the processes of growth of the protoplasm, formation of material for secretion, and discharge from the cell may all go on simultaneously, the material becoming formed by or from the cell-protoplasm on the one hand, and discharged on the other hand into the commencement of the duct.

The material which accumulates within the cell is not always the same as that which appears in the discharged secretion. Thus in the glands which furnish the digestive ferments—especially the gastric glands and the pancreas—it has

been shown that the material which appears in the form of granules within the cells is not the pepsin and the trypsin which respectively characterise the secretions of those glands, but a precursor which is termed "zymogen," and is easily transformed into the ferments by the action of certain reagents; and it is supposed that a similar change may occur during the discharge of the secretion from the cells. Again in the cells which secrete mucus, the clear substance which accumulates within the cells is not mucin, but a precursor of mucin, which is termed "mucigen," from the facility with which it becomes on discharge converted into mucin.

It is difficult to decide whether the material for secretion is formed by the direct conversion of a part of the protoplasm of the secreting cell, or from materials taken up from the plasma of the blood and elaborated by the agency of the protoplasm. It is generally assumed that the former is the case, and that the protoplasm of the cells of a secreting gland increases in amount as the first stage in the process of formation of the secretion. But since the materials of secretion accumulate in the substance of the protoplasm it may not be always possible to determine how much of the increase of size of the cell is due to a growth of the protoplasm itself, and how much to the accumulation of the materials of secretion, either entirely or only partially elaborated, within it. It is probable that the reticular structure which the protoplasm of many secreting cells exhibits is caused by the accumulation within it of the material of secretion in a granular or globular form; the closely-arranged globules reducing the protoplasm in which they are embedded to the condition of a fine spongework.

The secretory changes which have heen noticed by various observers in the cells of different glands will be more fully described when the several glands are specially treated of.

Modifications in form of the secreting surface.—A secreting apparatus, effectual for the purpose which it is destined to fulfil, may thus be said essentially to consist of a layer of secreting cells

Fig. 214.

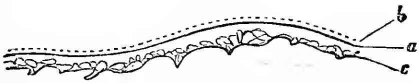


Fig. 214.—PLAN OF A SECRETING MEMBRANE (Sharpey).

a, membrana propria or basement-membrane; *b*, epithelium, composed of secreting cells; *c*, layer of capillary blood-vessels.

covering a free surface, whilst a layer of finely ramified blood-vessels is spread out close to the attached ends of the cells, with sometimes a basement membrane between the two. But whilst the structure may remain essentially the same, the configuration of the secreting surface presents various modifications in different secreting organs. In some cases, the secreting surface is plain (fig. 214), or, at least, expanded, as in various parts of the serous, synovial, and mucous membranes, which may be looked on as examples of comparatively simple forms of secreting apparatus; but, in other instances, and particularly in the special secretory organs named glands, the surface of the secreting membrane is variously involved and complicated. An obvious effect of this complication is to increase the extent of the secreting surface in a secreting organ within a given bulk, and thus augment the quantity of secretion yielded by it. No connection has been clearly shown to exist between the *quality* of the secretion and the particular configuration, either internal or external, of the organ;

on the other hand, we know that the same kind of secretion that is derived from a complex organ in one animal, may be produced by an apparatus of most simple form in another.

There are two principal modes by which the surface of the membrane is so increased in extent, namely, by rising or protruding in form of a prominent fold or some otherwise shaped projection (fig. 215, *d*, *e*), or by retiring, in form of a recess (fig. 216, A, *g*, *h*).

The first-mentioned mode of increase, or that by *protrusion*, is not that which is most generally followed in nature, still it is not without example, and, as instances, may be cited the Haversian fringes of the synovial membranes and the urinary organ of molluscs. In these cases, the membrane assumes the form of projecting folds, which, for the sake of further increase of surface, may be again plaited and complicated, or cleft and fringed, at their borders (fig. 215, *e*, *f*).

The augmentation of the secreting surface by *recession* or *inversion* of the membrane, in the form of a cavity, is, with few exceptions, that generally adopted in the construction of secreting glands. The first degree is represented by a simple recess (fig. 216, *g*, *h*), and such a recess, formed of secreting membrane, constitutes a *simple gland*. The

Fig. 215.

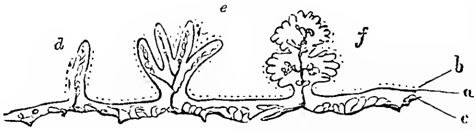


Fig. 215.—Plan to show augmentation of surface by formation of processes (Sharpey).

a, *b*, *c*, as in preceding figure; *d*, simple, and *e f*, branched or subdivided processes.

shape of the cavity may be tubular (*g*) or saccular (*h*): of these two kinds of simple gland the former is by far the more common. Examples of simple glands are found at the back of the tongue, in the intestines, and in the olfactory membrane. The secreting surface may be increased, in a simple tubular gland, by mere lengthening of the tube, in which case, however, when it acquires considerable length, the tube is coiled up into a ball (fig. 216, *i*), so as to take up less room, and adapt itself to receive compactly ramified blood-vessels. The sweat-glands of the skin are instances of simple glands formed of a long convoluted tube. But the chief means observed of further increasing the secreting surface is by the subdivision, as well as extension, of the cavity, and when this occurs the gland is said to be *compound*. There is, however, a condition sometimes met with, in which the sides or extremity of a simple tube or sac merely become pouched or loculated (fig. 216, *k*, *l*).

In the compound glands, the divisions of the secreting cavity may assume a tubular or a saccular form, and this leads to the distinction of these glands into the "tubular," and the "saccular," or "racemose." Glands which are intermediate in structure between these types are also met with, and have received the name of "acino-tubular" glands, since in them the terminal saccules or acini present a more or less tubular form.

The *racemose* compound glands (fig. 216, C) contain a multitude of

saccules, opening in clusters into the extremities of a branched tube, named the excretory duct. The saccules are rounded, pyriform or thimble-shaped. They are often rather filled than lined by secreting cells; they are arranged in groups, round the commencing branches of the duct, into which they open (fig. 216, C, *n*); or it might with equal truth be said that the branches of the duct are distended into clusters of saccular dilatations. The ultimate branches of the duct open into larger branches (*o*), these into larger again, till they eventually terminate in one or more principal excretory ducts (*m*), by which the secretion is poured out of the gland. It is from the clustered arrangement of their ultimate vesicular recesses that these glands are named "racemose" or grape-like; and they, for the most part, have a distinctly lobular structure. The lobules are held together by the branches of the duct

Fig. 216.

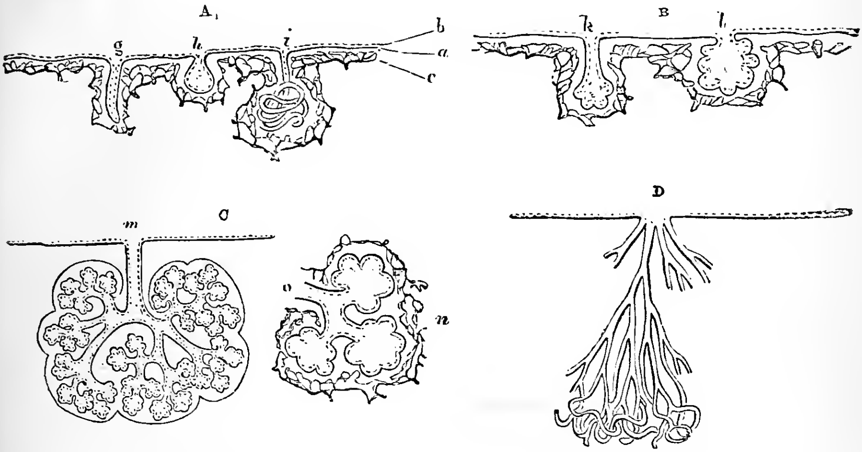


Fig. 216.—PLANS OF EXTENSION OF SECRETING MEMBRANE, BY INVERSION OR RECESSION. (Sharpey.)

A, simple glands, viz., *g*, straight tube; *h*, sac; *i*, coiled tube. B, simple glands with loculated walls; *k*, of tubular form; *l*, saccular. C, racemose, or saccular compound gland; *m*, entire gland, showing branched duct and lobular structure; *n*, a lobule, detached with *o*, branch of duct proceeding from it. D, compound tubular gland.

to which they are appended, and by interlobular connective tissue which also supports the blood-vessels in their ramifications. The larger lobules are made up of smaller ones, these of still smaller, and so on for several successive stages. The smallest lobules (*n*) consist of two or three groups of saccules, with a like number of ducts, joining into an immediately larger ramuscule (*o*), which issues from the lobule; and a collection of the smallest lobules, united by connective tissue and vessels, forms one of the next size, which, too, has its larger branch of the duct, formed by the junction of the ramuli belonging to the ultimate lobules. In this way, the whole gland is made up, the number of its lobules and of the branches of its duct depending on its size; for whilst some glands of this kind, like the

parotid, consist of innumerable lobules, connected by a large and many-branched duct, others, such as some of the sebaceous glands of the skin, are formed of but two or three ultimate lobules, or even of a single one. In fact, a small racemose gland resembles a fragment of a larger one.

The smallest lobules were originally called *acini*, a term which is now generally used to denote the saccular recesses in the lobules. These are also termed *alveoli.*

The ultimate saccules of a racemose gland are lined, and sometimes almost filled by the secreting cells, a cavity being left in the centre communicating with the excretory duct (fig. 217). In some cases, minute canals lead from the central cavity between the cells, and these may aid in the conveyance of the secretion of the latter into the

Fig. 217.

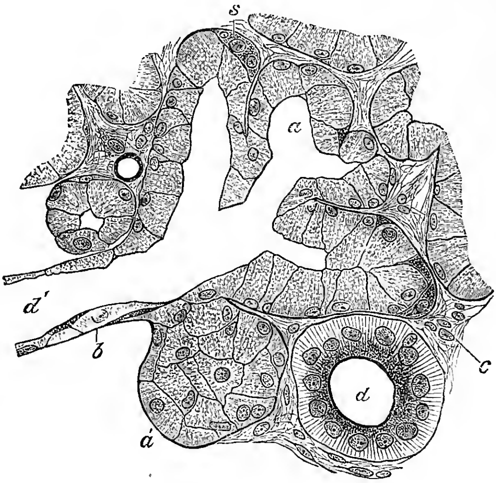


Fig. 217.—Section of a racemose gland, showing the commencement of a duct in the alveoli. Magnified 425 diameters (E. A. S.).

a, one of the alveoli, several of which are in the section shown grouped around the commencement of the duct, *d'*; *a'*, an alveolus, not opened by the section; *b*, basement membrane in section; *c*, interstitial connective tissue of the gland; *d*, section of a duct which has passed away from the alveoli, and is now lined with characteristically-striated columnar cells; *s*, semilunar group of darkly-stained cells at the periphery of an alveolus.

cavity. It is doubtful whether these intercellular canals have proper walls or are merely formed by the juxtaposition of grooves on the adjacent sides of the cells. Further, the flattened cells which compose the basement-membrane may send delicate lamellar processes between the alveolar cells, among which they form a sustentacular network (Boll, Ebner).

Many glands, yielding very different secretions, belong to the racemose class. As examples, it will be sufficient to mention the salivary, lachrymal, and mammary glands, and many of the small glands which open into the mouth, fauces, and windpipe; but some even of these are intermediate in structure between the true racemose and the tubular glands.

Of the *tubular* compound glands, the most characteristic examples are the testis and kidney. In these the tubular ducts divide again and again into branches, which, retaining their tubular form, are greatly lengthened out. The branches of the ducts are formed, as usual, of a limitary or basement-membrane (*membrana propria*), lined by epithelium, and in contiguity, by its outer surface, with capillary blood-vessels. By the multiplication and elongation of the tubular branches a vast extent of secreting surface is obtained, the tubes being usually coiled up into a compact mass, which is traversed and held together by blood-vessels, and sometimes, also, divided into lobules and supported, as in the testis, by fibrous partitions, derived from the inclosing capsule of the gland. In consequence of their intricately involved arrangement, it is sometimes difficult to find out how the tubular ducts are disposed at their extremities. In the testis some are free, and simply closed without dilatation, and others anastomose with neighbouring tubes, joining with them in the form of loops ; in the kidney, little round tufts of fine blood-vessels project into terminal dilatations of the ducts, but without piercing the basement membrane.

The mammalian liver does not precisely agree in structure with either of the above classes of compound glands. Its secreting cells are collected into small polyhedral masses termed the hepatic lobules, pervaded by a network of capillary blood-vessels ; and the ducts begin within the lobules, in the form of a network of exceedingly fine channels which run between the sides of contiguous cells.

Besides blood-vessels, the glands are furnished with lymphatics, which in most compound glands proceed from interstitial lymphatic spaces which surround the alveoli as already stated (p. 203). Branches of nerves have also been followed for some way into these organs ; and that an influence is exerted on secreting organs through the medium of the nervous system, is shown by the fact, that the flow of secretion in several glands is affected by mental emotions, and that the flow of secretion from many glands may be brought on by direct or reflex stimulation of their nerves. In some cases also an increased accumulation of the materials of secretion within the cells, may thus be produced. Moreover, fine non-medullated nerve-fibres have in several instances been described as entering between the cells of the alveoli ; and in the salivary glands, Pflüger has affirmed a direct passage of nerve-fibres, both medullated and non-medullated, into the secreting cells. His observations, however, have not been confirmed by other inquirers, although Kupffer has described a similar connection between nerve-fibres and secreting cells in the salivary glands of insects.

Uniting the several parts of a compound gland is a certain amount of interstitial connective tissue, which varies in character in different glands, being in some more fibrous, in others more cellular, and in others again being represented by retiform tissue.

Some glands have a special envelope, as in the case of the kidney and testis.

The ducts of glands ultimately open into cavities lined by mucous membrane, or upon the surface of the skin. They are sometimes provided with a reservoir, in which the secretion is collected, to be discharged at intervals. The reservoir of the urine receives the whole of the secreted fluid ; in the gall-bladder, on the other hand, only a part of the bile is collected. The vesiculæ seminales afford another example of these

appended reservoirs. The ducts are constructed of a basement-membrane and lining of epithelium, and in their smaller divisions there is nothing more ; but in the larger branches and trunks, a coat, composed of connective tissue, with which in some cases involuntary muscular fibres are introduced, is added. In the ducts of the sweat glands, the muscular fibres lie between the basement-membrane and the epithelium. The epithelium-cells are usually flattened at the commencement of the duct, where these emerge from the alveoli, and are columnar in the rest of the duct. In some glands the columnar cells of the ducts exhibit the peculiar striated appearance before referred to (see p. 4), in the part of the cell next to the basement-membrane, and the alveolar cells may also exhibit a similar appearance, but far less distinctly.

Mechanism of the discharge of secretion from a gland.—Although no doubt dependent ultimately upon physical and chemical conditions, it is not known precisely in what way the discharge of secretion from the gland-cells, and eventually from the gland is effected. The forces which produce the discharge are, however, considerable, and are influenced as we have seen through the nervous system. In the cutaneous glands of the frog Stricker and Spina have noticed that irritation of the nerves is followed by swelling and enlargement of the previously flattened cells of the gland, and that this enlargement causes a discharge of secretion from the mouth of the duct. The swelling is produced by an accumulation of fluid, derived from the plasma of the blood, within the cells, and when these come again to the condition of rest and resume the flattened form, the fluid is supposed to pass from them into the cavity of the alveolus, carrying with it the materials of secretion extracted from the cells. If the glands are again stimulated the same process is gone through, and in this way it is supposed an intermittent discharge may be caused. There is no evidence, however, to show that similar changes occur in other glands, nor is it explained how it happens that the water of the plasma should pass into the cells only under the influence of excitation.

The discharge from the ducts of a gland is partly due to the *vis-a-tergo* of the accumulating secretion, partly to the peristaltic contraction of the muscular tissue in the wall of the duct (where this tissue exists).

Recent Literature.—The following authors have written more recently on the structure of secreting glands and on the changes which their cells undergo during secretion :—*Gianuzzi*, in Ber. d. sächs. Gesellsch. d. Wissensch., 1862 ; *Boll*, in Arch. f. mikr. Anat., 1868 and 1869 ; *R. Heidenhain*, Studien d. phys. Inst. zu Breslau, 1868 ; Pflüger's Arch., 1875, and article "Absonderung," in Hermann's Handb., 1880 ; *Ebstein*, in Arch. f. mikr. Anat., 1870 ; *Pflüger*, Article "Salivary Glands," in Stricker's Handbook, 1871 ; *Ebner*, in Arch. f. mikr. Anat., 1872, and Die acin. Drüsen der Zunge, 1873 ; *Kupffer*, in Ludwig's Festgabe, 1874 ; *Watney*, in Proc. Roy. Soc., 1874 ; *Swiecicki*, in Pfl. Arch., 1876 ; *Lavdorsky*; *Nussbaum* ; *Partsch*, in Arch. f. mikr. Anat., 1877 ; *Kühne u. Lea*, in Heidelberg Verhandl., 1877 ; *Grützner*, in Pfl. Arch. 1879 ; *Langley*, in Journal of Physiology, 1879 ; with *Sewall*, in the same Journal ; also in Phil. Trans., 1881.

MUCOUS MEMBRANES.

These membranes, unlike the serous, line passages and cavities which communicate with the exterior, as well as recesses, ducts and receptacles of secretion, which open into such passages. They are habitually subject either to the contact of foreign substances introduced into the body, such as air and aliment, or of various secreted or excreted matters, and hence their surface is coated over and protected by mucus, a fluid of a more consistent and tenacious character than that which moistens the serous membranes.

The mucous membranes of several different or even distant parts are continuous, and they may all, or nearly all, be reduced to two great divisions, namely the *gastro-pneumonic* and *genito-urinary*. The former covers the inside of the alimentary and air-passages as well as the less considerable cavities communicating with them. It may be described as commencing at the edges of the lips and nostrils, where it is continuous with the skin, and proceeding through the nose and mouth to the throat, whence it is continued throughout the whole length of the alimentary canal to the termination of the intestine, there again meeting the skin, and also along the windpipe and its numerous divisions as far as the air-cells of the lungs, to which it affords a lining. From the nose the membrane may be said to be prolonged into the lachrymal passages, extending up the nasal duct into the lachrymal sac and along the lachrymal canals until, under the name of the conjunctival membrane, it spreads over the fore part of the eyeball and inside of the eyelids, on the edges of which it meets with the skin. Other offsets from the nasal part of the membrane line the frontal, ethmoidal, sphenoidal and maxillary sinuses, and from the upper part of the pharynx a prolongation extends on each side along the Eustachian tube to line that passage and the tympanum of the ear. Besides these there are offsets from the alimentary membrane to line the salivary, pancreatic, and biliary ducts, and the gall-bladder. The *genito-urinary* membrane invests the inside of the urinary bladder and the whole tract of the urine in both sexes, from the interior of the kidneys to the orifice of the urethra, also the seminal ducts and vesicles in the male, and the vagina, uterus and Fallopian tubes in the female.

By one surface the mucous membranes are attached to the parts which they line or cover, by means of areolar tissue, named "submucous," which differs greatly in quantity as well as in consistency in different parts. The connection is in some cases close and firm, as in the cavity of the nose and its adjoining sinuses; in other instances, especially in cavities subject to frequent variation in capacity, like the gullet and stomach, it is lax and allows some degree of shifting of the connected surfaces. In such cases as the last-mentioned the mucous membrane is accordingly thrown into folds when the cavity is narrowed by contraction of the exterior coats of the organ, and of course these folds, or *rugæ* as they are named, are effaced by distension. But in certain parts the mucous membrane forms permanent folds, not capable of being thus effaced, which project conspicuously into the cavity which it lines. The best-marked example of these is presented by the *valvulæ conniventes* seen in the small intestine. These, as is more fully described in the special anatomy of the intestines, are crescent-shaped duplicatures of the

membrane, with connecting areolar tissue between their laminæ, which are placed transversely and follow one another at very short intervals along a great part of the intestinal tract. The chief use of the valvulæ conniventes is doubtless to increase the surface of the absorbing mucous membrane within the cavity.

In most situations the mucous membranes are nearly opaque or only slightly translucent. They possess no great degree of tenacity and but little elasticity, and hence are readily torn by a moderate force. The redness which they commonly exhibit during life, and retain in greater or less degree in various parts after death, is due to the blood contained in their vessels. The degree of redness is greater in the fœtus and infant than in the adult. It is greater too in certain situations; thus, of the different parts of the alimentary canal, it is most marked in the stomach, pharynx, and rectum.

Structure.—A mucous membrane is composed of *corium* and *epithelium*. The *epithelium* covers the surface. The membrane which remains after its removal is named the *corium*, as in the analogous instance of the true skin.

The **epithelium** (fig. 218, *e*) is the most constant part of a mucous membrane, being continued over certain parts to which the other constitutents of the membrane cannot be traced, as over the alveoli of the lungs, and the front of the cornea of the eye. It may be scaly and stratified as in the mouth and throat, columnar as in the intestine, or ciliated as in the respiratory tract and uterus. When a mucous membrane is covered with an epithelium of the scaly and stratified variety, the mucus which moistens its surface is derived from glands in the membrane, which are lined with columnar and polyhedral secreting cells; but when a columnar epithelium covers the surface, a large part of the mucus is formed in the cells of this layer, and the glands of the membrane are frequently devoted to the elaboration of some special secretion.

Those columnar cells which are especially concerned in the production of mucus often become greatly distended with the accumulated mucigen into the shape of a goblet or chalice, and this may in many be seen to have become exuded from the free and apparently open end of the cell as a droplet of mucus (see p. 44). A certain number of these *goblet-* or *chalice-cells* are almost always to be found amongst the ordinary columnar cells. It is somewhat uncertain whether after discharge of their secretion they become converted into ordinary columnar cells, or whether they permanently maintain the chalice-like form, their cavity becoming again filled with secretion during rest. If the latter is the case the cells in question are analogous to the uni-cellular glands which are met with in the integument of some of the lower animals (leech).

The **corium** of a mucous membrane consists of connective tissue, either simply areolar or containing a large intermixture of lymphoid tissue. It is usually bounded next the epithelium by a basement membrane (fig. 218, *bm*), and next the submucous tissue by a thin layer of non-striated muscular tissue termed the *muscularis mucosæ* (*mm*).

The *basement membrane* is not everywhere demonstrable, but where it is well marked it appears in section as a thin line immediately underlying the epithelium. Viewed on the flat and with the superjacent epithelium removed, the membrane in question seems at first sight homogenous; but treatment with nitrate of silver brings to view the

outlines of the flattened cells of which it is in reality composed. It is not always a complete membrane, for in some parts the cells composing it, instead of adhering closely by their edges, intercommunicate by branching processes so as to form a network instead of a continuous membrane. The basement membrane follows all the eminences and depressions of the surface of the mucous membrane, dipping down to take part in the formation of the wall of the glands, and passing over the raised villi and other prominences.

Fig. 218.

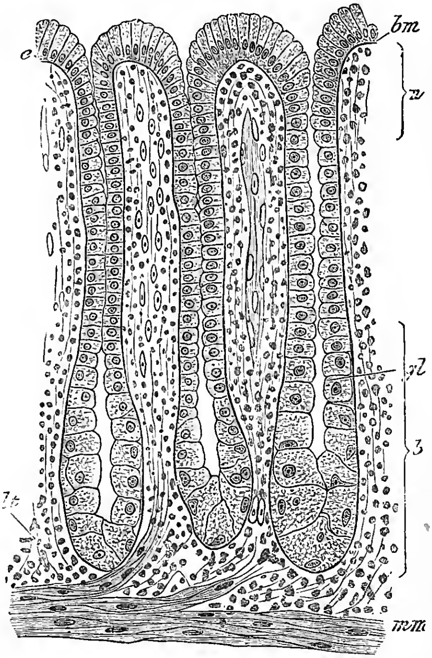


Fig. 218.—Section of mucous membrane from the stomach of the kangaroo. Magnified about 260 diameters (E. A. S.).

e, columnar epithelium of the surface, continued into the neck, *n*, of the simple tubular glands, *gl*; but becoming at first cubical, and then polyhedral towards the base, *b*, of the glands; *lt*, lymphoid tissue of the corium, seen also between the glands; *bm'*, basement membrane, bounding the corium superficially; *mm*, muscularis mucosæ, bounding the mucous membrane at its attached surface, and sending small bundles of plain muscular tissue between the glands. The commencement of a lymphatic vessel is shown between two of the glands, but its connection with deeper lymphatics was not seen. The blood-vessels of the membrane are not represented.

The *muscularis mucosæ* forms the deepest part of a mucous membrane, but it is not everywhere present. It is best developed in the mucous membrane of the alimentary canal, in some parts of which it may consist of two layers, in the one of which the fibres are longitudinal, in the other circular in direction. From its inner surface muscular bundles bend inwards into the thickness of the mucous membrane, passing between the glands contained within it, and even into its prominences, so as in many cases to reach and become attached to the basement-membrane covering them. The muscularis mucosæ is a part therefore of the mucous membrane, and is not to be confounded with the muscular coat proper, which forms a separate layer in most of the hollow viscera.

The *connective tissue layer* or *corium proper* varies much in structure in different parts. In some situations, as in the gullet, bladder, and vagina, the filamentous connective tissue is abundant, and extends throughout its whole thickness, forming a continuous and tolerably compact web, and rendering the mucous membrane of those parts comparatively stout and tough. In the stomach and intestines, on the other hand, where the membrane is pervaded by tubular glands, the tissue between these is chiefly retiform or lymphoid tissue (fig. 218, *lt*) with but

few white and elastic fibres, and hence in these situations the membrane, although thicker, is far less firm and tough than in parts where much of the white connective tissue is found. In other mucous membranes transitions are met with between these two extremes.

It frequently happens that in certain circumscribed places the lymphoid tissue is greatly increased in amount, and becomes densely packed with lymphoid cells. In this way the so-called *solitary glands, follicles* or *nodules* are produced. If there be many lymphoid nodules adjacent to one another, so as to make up a localized patch, a so-called agminated gland is formed, or if massed together more thickly, a lymphoid organ like the tonsil. These collections of lymphoid tissue, which may if large extend, on the one hand, down into the submucous tissue, and on the other, upwards into the epithelium, have been already referred to (p. 213), and will be more particularly described when the several parts in which they occur come under consideration.

Blood-vessels are abundant in most mucous membranes. The branches of the arteries and veins, dividing in the submucous tissue, send smaller branches into the corium, which divide to form a network of capillaries in the latter. This capillary network lies immediately beneath the epithelium, or the basement-membrane when this is present, advancing into the villi and papillæ to be presently described, and surrounding the tubes and other glandular recesses. The **lymphatics** also form networks of cleft-like vessels in the mucous membrane, which communicate with plexuses of larger valved vessels in the submucous tissue; they commence either by blind diverticula, as in the villi, or in the form of a superficial network, which is almost always more deeply placed than the network of blood-capillaries. The lymphatic vessels often form sinus-like dilatations around the bases of the lymphoid nodules.

The **nerves** of mucous membranes seem chiefly to be distributed to the muscularis muscosæ where this exists. Before proceeding to their destination they are in many parts collected together to form a gangliated plexus in the sub-mucous tissue, such as the plexus of Meissner in the alimentary canal. Some nerves pass however to the epithelium and terminate between the epithelial cells; at least this has been shown to be the case in the stratified epithelium which covers the mucous membrane of the palate in the rabbit, and in that which lines the vagina of the same animal.

Papillæ and villi.—The free surface of the mucous membranes is in some parts plain, but in others is beset with little eminences named papillæ and villi. The *papillæ* are best seen on the tongue; they are small processes of the corium, mostly of a conical or cylindrical figure, containing blood-vessels and nerves, and covered with epithelium. Some are small and simple, others larger and covered with secondary papillæ. They serve various purposes; some of them no doubt minister to the senses of taste and touch, many appear to have chiefly a mechanical office, while others would seem to give greater extension to the surface of the corium for the production of a thick coating of epithelium. The *villi* are most fully developed on the mucous coat of the small intestines. Being set close together like the pile of velvet, they give to the parts of the membrane which they cover the aspect usually denominated "villous." They are in reality little elevations or processes of the corium, covered with epithelium, and

containing bloodvessels and lacteals, which are thus favourably disposed for absorbing nutrient matters from the intestine. The more detailed description of the papillæ and villi belongs to the special anatomy of the parts in which they occur.

In some few portions of the mucous membranes the surface is marked with fine ridges which intersect each other in a reticular manner, and thus inclose larger and smaller polygonal pits or recesses. This peculiar character of the surface of the membrane, which has been termed "alveolar," is seen very distinctly in the gall-bladder, and on a finer scale in the vesiculæ seminales ; still more minute alveolar recesses with intervening ridges may be discovered with a lens on the mucous membrane of the stomach.

Glands of mucous membranes.—Many, indeed most, of the glands of the body pour their secretions into the great passages lined by mucous membranes ; but there are certain small secreting glands which may be said to belong to the membrane itself, inasmuch as they are found in numbers over large tracts of that membrane, and yield mucus, or special secretions known to be formed in particular portions of the membrane. Omitting local peculiarities the glands referred to may be described as of two kinds, viz.:—

I. *Tubular glands.*—These are minute tubes formed by recesses or inversions of the basement membrane, and lined with epithelium (fig. 218, *gl*). They are usually placed perpendicularly to the surface, and often very closely together, and they constitute the chief substance of the mucous membrane in those parts where they abound, its thickness depending on the length of the tubes, which differs considerably in different regions. The tubes open by one end on the surface ; the other end is closed, and is either simple or cleft into two or more branches. The tubular glands are abundant in the stomach, and in the small and large intestines, where they are comparatively short and known as the crypts of Lieberkühn. They exist also in considerable numbers in the mucous membrane of the uterus.

II. *Small compound glands.*—Under this head are here comprehended minute compound glands of the racemose or of the acino-tubular kind, with branched ducts of various lengths, which open on the surface of the membrane. Numbers of these, yielding some a mucous, others a more albuminous or serous secretion, open into the mouth and windpipe. To the naked eye they have the appearance of small solid bodies, often of a flattened lenticular form, but varying much both in shape and size, and placed at different depths below the mucous membrane on which their ducts open. The glands of Brunner, which form a dense layer in the commencing part of the duodenum, belong to this category.

Mucus—the secretion which moistens the surface of a mucous membrane—is a viscid transparent fluid, which when examined by the microscope is generally found to contain, besides detached epithelium cells, rounded cells named mucus-corpuscles, which closely resemble the pale corpuscles of the blood, and are probably identical with them (having wandered either from the vessels or from the lymphoid tissue of the membrane). The chief organic constituent of mucus—mucin—is precipitated from the fluid by the addition of acids.*

* The several mucous membranes are described more in detail when the organs of which they form a part are treated of, and the works which refer to them may then also be mentioned most appropriately.

THE SKIN.

The skin consists of the cutis vera or corium, and the cuticle or epidermis.

The **Epidermis, Cuticle, or Scarf-Skin** belongs to the class of stratified epithelia, the general nature of which has been already considered. It forms a protective covering over every part of the true skin.

Fig. 219.

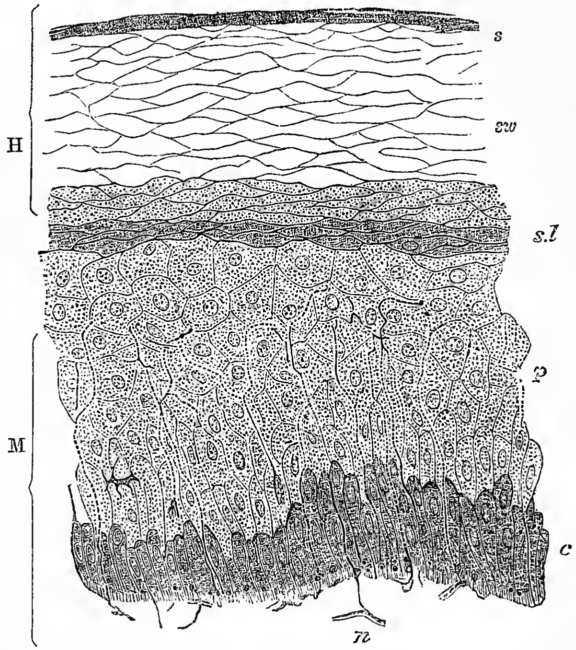


Fig. 219.—Section of epidermis from the human hand. Highly magnified (Ranvier).

H, horny layer, consisting of *s*, superficial horny scales; *sw*, swollen-out horny cells; *s.l*, stratum lucidum; *M*, rete mucosum or Malpighian layer, consisting of *p*, prickle-cells, several rows deep; and *c*, elongated cells forming a single stratum near the corium. The granular cells of Langerhans, which lie just below the stratum lucidum, are not shown. *n*, part of a plexus of nerve-fibres in the superficial layer of the cutis vera. From this plexus, fine varicose nerve-fibrils may be traced passing up between the cells of the Malpighian layer.

The thickness of the cuticle varies in different parts of the surface, measuring in some places not more than $\frac{1}{240}$th, and in other parts, as much as $\frac{1}{24}$th of an inch (about a millimeter), or even more than this in some individuals. It is thickest in the palms of the hands and soles of the feet, where the skin is much exposed to intermittent pressure, and it is not improbable that such pressure may serve to stimulate the subjacent true skin to a more active formation of epidermis; but the difference does not depend immediately on external causes, for it is well marked even in the fœtus.

The more firm and transparent superficial part, or horny layer, of the

epidermis, may be separated after maceration from the deeper, softer, more opaque, and recently formed part, which constitutes what is called the Malpighian layer, or *rete mucosum.*

The under or attached surface of the cuticle is moulded on the adjoining surface of the corium, and, when separated by maceration or putrefaction, presents impressions corresponding exactly with the papillary or other eminences, and the furrows or depressions of the true skin; the more prominent inequalities of the latter are marked also on the outer surface of the cuticle, but less accurately. Fine tubular prolongations of the cuticle sink down into the ducts of the sweat-glands, and are often partially drawn out from their recesses when the cuticle is detached, appearing then like threads proceeding from its under surface.

Structure.—The cuticle is made up of cells agglutinated together in many irregular layers. The deepest cells are elongated in figure, and placed perpendicularly on the surface of the corium (fig. 219 *c*, and fig. 224); they are denticulate at their lower ends, and fit into corresponding fine denticulations of the corium. The perpendicular cells generally form one stratum; above them are cells of a more rounded or polyhedral shape (*p*). These, as first shown by Max Schultze and Virchow, are marked on their surface with numerous ridges and furrows or are covered

Fig. 220.

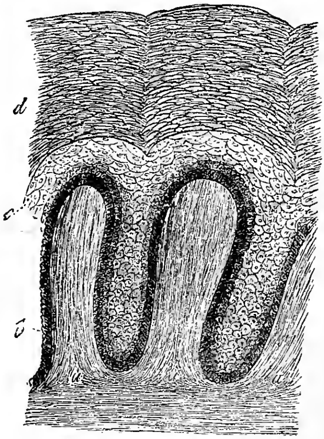


Fig. 220.—Skin of the Negro, vertical section, magnified 250 Diameters (Kölliker).

a, a, cutaneous papillæ; *b,* undermost and dark-coloured layer of oblong vertical epidermis-cells; *c,* mucous or Malpighian layer; *d,* horny layer.

with minute spines. The spines and ridges of neighbouring cells do not, however, interlock one with another as was at first supposed, but on the contrary, meet at their summits so as to leave between the cells fine channels through which it is conceived nutrient plasma may be conducted to the cells (Bizzozero). These so-called "prickle-cells" form several strata; above, they become gradually more flattened, conformably to the surface, until a layer is reached in which the outlines of the cells, which are two or three deep, are indistinct, so that in section they appear to form a clear almost homogeneous layer (*stratum lucidum*, Oehl; fig. 219, *s.l*). Immediately below the stratum lucidum a layer, often incomplete, of granular-looking, flattened cells is usually to be seen (Langerhans). The granules in these cells are composed of a peculiar matter staining deeply with carmine, and they are thought by some to have an intimate relation to the formation of the horny substance in the more superficial cells. Immediately above the stratum lucidum, which may be looked upon as the commencement of the horny layer of the epidermis, is a stratum of considerable thickness in which the cells are much enlarged, and the nuclei in many cases no longer visible (*sw*): towards the surface they pass into

the hard flattened scales (*s*) which are to be thrown off by desquamation. As the cells change their form, they undergo chemical and physical changes in the nature of their contents; for in the deeper layers they consist of a soft, granular, protoplasmic matter, soluble in acetic acid, whilst the superficial ones are transparent, dry, and horny, and are not affected by that reagent. These dry hard scales may be made to reassume their cellular form, by exposure for a few minutes to a solution of caustic potash or soda, and then to water. Under this treatment they are softened by the alkali, and distended by imbibition of water.

Many of the cells of the cuticle contain pigment-granules, and often give the membrane more or less of a tawny colour, even in the white races of mankind; the blackness of the skin in the negro depends entirely on the cuticle. The pigment is contained principally in the cells of the deep layer or rete mucosum (fig. 220), and appears to fade as the cells approach the surface, but even the superficial part possesses a certain degree of colour.

In the intercellular channels of the Malpighian layer lymph-corpuscles, rounded or branched, are occasionally observed. They are in all probability derived from the subjacent corium.

Nerves.—Fine varicose nerve-fibrils pass up into the epidermis, penetrating between the cells of the Malpighian layer (fig. 219), where they undergo a certain amount of ramification. The branches do not unite with one another to form a network, but end in knob-like swellings or varicosities. With the growth and displacement of the cells between which they are placed, these varicosities become, according to Ranvier, continually detached from the end of the fibrils, the latter meanwhile growing constantly to supply the place of the detached portions.

In the skin covering the snout of certain animals (*e.g.* mole) the nerves end in peculiar terminal organs (Eimer), formed of thickenings of the epidermis, the nerve-fibres passing as an elongated bunch of closely set, somewhat zigzag, varicose, unbranched fibrils between the epidermis-cells. Besides these fibrils there are others at the periphery of the organ which are less closely arranged, and terminate in branched extremities as in other parts of the epidermis.

Merkel has described the nerves of the epidermis as ending in pyriform cells (tactile cells) placed between the ordinary epithelial cells; and others have thought that the nerves could be traced to stellate cells in the interstitial spaces, but improved methods of staining with chloride of gold which have been employed in the investigation would seem to render it probable that the termination of the nerve-fibrils in the cuticle is always free as above described.

Formation and growth of Epidermis.—In the earliest condition of the embryo there is a special layer of cells, the ectoderm or epiblast, set aside chiefly for the production of the epidermis; and it is probable, that the subsequent generations of epidermic cells by which the tissue is throughout life maintained, are derived by unbroken descent from the original embryonic stratum. At first the cells form a single columnar layer, but by division of its cells a horny layer early makes its appearance, being represented at first by but a single layer of large polygonal cells, covering the layer of smaller and more columnar cells (Kölliker). The latter soon divide again and produce a second row of rounded cells superficial to them, and the increase of thickness which is thus begun continues by further division of cells in the deeper layers, so that before long the Malpighian layer has become extremely well marked. Meanwhile its more superficial cells, undergoing a chemical transformation and becoming flattened out, have been added on to the under surface of the horny layer, and this change proceeds until the mucous and horny layers are about of equal thickness. After a time the superficial cells of the horny layer begin to desquamate, and this process goes on during the rest of fœtal life, the cast-off scales appearing partly in the liquor amnii, and also,

mixed with the secretion of the sebaceous glands, forming the so-called vernix caseosa covering the whole surface of the fœtus.

The pigment of the Malpighian layer in the coloured races of mankind frequently does not appear until a day or two after birth.

The growth of epidermis continues throughout life. The cells of the Malpighian layer are constantly undergoing multiplication, and the new cells thus produced push outwards those which are previously formed. The more superficial cells of the Malpighian layer are thus continually passing on to reinforce the horny layer, the cells as they proceed outwards becoming flattened and transformed into horny matter. This change seems to occur quite abruptly when the stratum lucidum is reached ; beyond this the cells again swell out somewhat, until on reaching the most superficial layers they are entirely transformed into structureless horny scales which are constantly undergoing desquamation.

There is reason to suppose that the regeneration of epidermis, when a portion has been removed by a blister or wound of any kind, takes place, like its growth, only from cells of the Malpighian layer. If the whole of the epidermis has been destroyed or removed over an extensive surface, the process of regeneration is very slow, since the new covering has to grow in from the epidermis at the margins of the wound. But if the deeper cells have not been wholly removed the regeneration may start from the places where any of them still remain, and the formation of the new covering is proportionately quicker. In the operation of skin-grafting so-called, the surgeon endeavours to transplant from a healthy portion of skin small pieces of the epidermis, including its deeper layers, to the denuded surface : if the operation succeed, each such graft acts as a centre from which the new formation of epidermis may spread, and in this way the raw surface may be much more speedily covered.

The **True Skin, Cutis Vera, Derma,** or **Corium,** is a sentient and vascular fibrous texture. It is covered and defended, as already explained, by the non-vascular cuticle, and is attached to the parts beneath by a layer of areolar tissue, named "subcutaneous," which, excepting in few parts, contains fat, and has therefore been called also the "panniculus adiposus" (fig. 221, *d*). The connection is in many parts loose and moveable, in others close and firm, as on the palmar surface of the hand and the sole of the foot, where the skin is fixed to the subjacent fascia by numerous stout fibrous bands, the space between being filled with a firm padding of fat. In some regions of the body the skin is moved by striated muscular fibres, which may be unconnected with fixed parts, as in the case of the orbicular muscle of the mouth, or may be attached beneath to bones or fasciæ, like the other cutaneous muscles of the face and neck, and the short palmar muscle of the hand.

Structure.—The cutis vera is made up of an exceedingly strong and tough framework of interlaced connective tissue fibres. The fibres are chiefly of the white variety, such as constitute the main part of the fibrous and areolar tissues, and are arranged in stout interlacing bundles, except at and near the surface, where the texure of the corium becomes finer and closer. With these are mixed elastic fibres, which vary in amount in different parts, and connective tissue corpuscles, which are often flattened up against the bundles of white fibres. Towards the attached surface the texure becomes much more open, with larger and larger meshes, in which lumps of fat and the sweat glands are lodged ; and thus the fibrous part of the skin, becoming more and more lax and more mixed with fat, blends gradually with the subcutaneous areolar tissue.

In consequence of this gradual transition of the corium into the subjacent tissue, it's thickness cannot be assigned with perfect precision.

As a general rule, it is thicker on the posterior aspect of the head, neck, and trunk, than in front; and thicker on the outer than on the inner side of the limbs, and as well as the cuticle, it is remarkably thick on the soles of the feet and palms of the hands. The skin of the female is thinner than that of the male.

The skin is generally said to measure from $\frac{1}{50}$th of an inch to nearly $\frac{1}{8}$th of an inch (·5 to 3 millimeters); but it has been pointed out by Warren that, on the back and shoulders, it may be as thick as 5 or 6 mm.; and here it is almost entirely formed of dense anastomosing bundles of connective tissue; sending down on the one hand fibrous prolongations through the subjacent panniculus adiposus, and being penetrated obliquely on the other hand by columns of fat cells, which extend from that layer to the bases of the small hair-follicles, and conduct blood-vessels to these and to the surface of the skin.

Bundles of plain muscular tissue are distributed in the substance of the corium wherever hairs occur; their connection with the latter will be afterwards explained. Muscular bundles of the same kind are

Fig. 221.

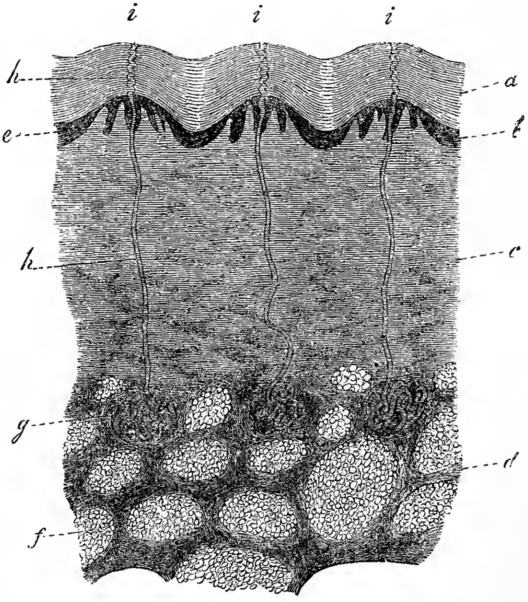


Fig. 221.—Vertical section of the skin and subcutaneous tissue, from the end of the thumb, across the ridges and furrows. Magnified 20 diameters (Kölliker).

a, horny, and *b*, Malpighian layer of the epidermis; *c*, corium; *d*, *panniculus adiposus*; *e*, papillæ on the ridges; *f*, fat-clusters; *g*, sweat-glands; *h*, sweat-ducts; *i*, their openings on the surface.

found in the subcutaneous tissue of the scrotum, penis, perineum, and areola of the nipple, as well as in the nipple itself. They join to form reticular layers, attached to the under surface of the corium. In the areola they are disposed circularly.

For convenience of description it is not unusual to speak of the

corium as consisting of two layers, the "reticular" and the "papillary.' The former, the more deeply seated, takes no part in the construction of the papillæ, but contains in its meshes hair follicles, cutaneous glands, and fat. The latter is extended into papillæ, and receives only the upper portion of the hair-follicles and glands, together with the terminal expansion of the blood-vessels.

The free surface of the cutis vera is marked in various places with larger or smaller furrows, which also affect the superjacent cuticle. The larger of them are seen opposite the flexures of the joints, as those so well known in the palm of the hand and at the joints of the fingers. The finer furrows intersect each other at various angles, and may be seen almost all over the surface; they are very conspicuous on the back of the hands. Fine curvilinear ridges, with intervening furrows, mark the skin of the palm and sole; these are produced by the ranges of papillæ, to be immediately described.

Papillæ.—The free surface of the corium is beset with small eminences thus named, which seem chiefly to contribute to the perfection of the

Fig. 222.

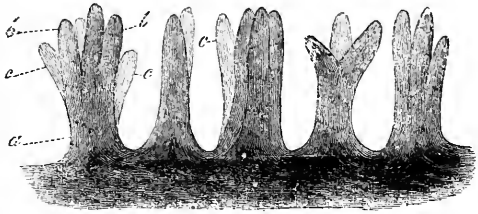


Fig. 222.—Compound papillæ from the palm of the hand, magnified 60 diameters.

a, basis of a papilla; *b*, *b*, divisions or branches of the same; *c*, *c*, branches belonging to papillæ of which the bases are hidden from view (after Kölliker).

skin as an organ of touch, seeing that they are highly developed where the sense of touch is exquisite. They serve also to extend the surface for the production of the cuticular tissue, and hence are large-sized and numerous under the nail. The papillæ are large, and in close array on the palm of the hand and palmar surface of the fingers, and on the corresponding parts of the foot. In these places they are ranged in lines forming the characteristic curvilinear ridges seen when the skin is still covered with its thick epidermis. They are of a conical figure, rounded or blunt at the top and sometimes cleft into two or more points, when they are named compound papillæ. They are received into corresponding pits on the under surface of the cuticle. In structure they resemble the rest of the superficial layer of the corium, and consist of a finely fibrillated tissue, with a few elastic fibres. On the palm, sole, and nipple, where they are mostly of the compound variety, they measure from $\frac{1}{200}$th to $\frac{1}{100}$th of an inch (0·125 to 0·25 mm.) in height. In the ridges, the larger papillæ are placed sometimes in single but more commonly in double rows, with smaller ones between them (fig. 221), that is, also on the ridges, for there are none in the intervening grooves. These ridges are marked at short and tolerably regular intervals with notches, or short transverse furrows, in each of which, about its middle, is the minute funnel-shaped orifice of the duct of a sweat-gland (fig. 223). In other

parts of the skin endowed with less tactile sensibility, the papillæ are smaller, shorter, fewer in number, and irregularly scattered. On the face they are reduced to from $\frac{1}{800}$ to $\frac{1}{500}$ of an inch; and here they at parts disappear altogether, or are replaced by slightly elevated reticular ridges. Fine blood-vessels enter most of the papillæ, forming either simple capillary loops in each, or dividing into two or more capillary branches, according to the size of the papilla and its simple or composite form, which turn round in the form of loops and return to the veins. Other papillæ receive nerves, to be presently noticed.

Blood-vessels and lymphatics.—The arteries divide in the subcutaneous tissue, and, as their branches pass from this deep expansion

Fig. 223.

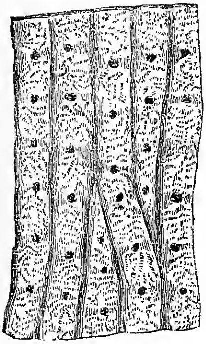


Fig. 223.—Magnified view of four of the ridges of the epidermis, with short furrows or notches across them: also the openings of the sudoriferous ducts (after Breschet).

towards the surface of the skin, they supply offsets to the fat-clusters, sweat-glands, and hair-follicles. They divide and anastomose again near the surface, and at length, on reaching it, form a network of capillaries, with polygonal meshes. Fine looped branches pass from the superficial arteries into the papillæ, as already mentioned. The veins closely accompany the arteries.

Lymphatics are found in all parts, although probably not everywhere in equal number; they are abundant and large in some parts of the skin, as on the scrotum and round the nipple. They form at least two networks, one superficial and another more deeply situated, which intercommunicate by uniting vessels, whilst the deeper net-work joins the lymphatics of the subcutaneous tissue. According to Klein there is a continuous plexus through the whole thickness of the corium, and all the vessels possess valves. The most superficial network, although close to the surface of the corium, is beneath the net of superficial blood-capillaries, which are much smaller than the lymphatic capillaries. In certain parts on the palm and sole, lymphatics pass into the papillæ, but do not reach their summits. Other lymphatics accompany the blood-vessels, two passing commonly with each small artery and vein, and joining and anastomosing over the vessels.

As in other kinds of connective tissue, the lymphatics of the skin may be said to originate in the cell-spaces of the tissue, and since the cells lie for the most part in rows between the bundles, the combined spaces form interfascicular clefts, which can be injected with the lymphatics. The superficial cell-spaces communicate with the intercellular channels of the epithelium, and thus these also are brought into connection with the lymphatics. The cell-spaces of the adipose tissue can similarly be injected.

Nerves.—Nerves are supplied in very different proportions to different regions of the skin, and according to the degree of sensibility. They pass upwards towards the papillary surface, where they form plexuses, of which the meshes become closer as they approach the surface, and the

constituent branches finer. From the most superficial plexus, which lies immediately under the epithelium, delicate non-medullated fibrils have been traced passing upwards amongst the cells of the Malpighian layer of the cuticle, where they end, as we have seen, in free slightly bulbous extremities. A large share of the cutaneous nerves is distributed to the hair-follicles, whilst some terminate in end-bulbs, tactile corpuscles, and Pacinian bodies, the last named being seated in the subcutaneous tissue. The tactile corpuscles of the skin are found most numerously in certain papillæ of the palm and sole, more sparingly in those of the back of the hand and foot, the palmar surface of the fore-arm, and the nipple. Such papillæ commonly contain no blood-vessels, and are named "tactile," (fig. 224, *b*), as distinguished from the "vascular" papillæ (*a*). The structure of these different terminal corpuscles has been already described

Fig. 224.

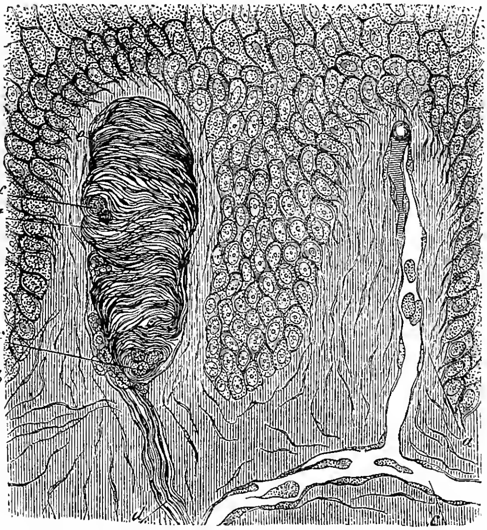


Fig. 224.—Section of skin showing two papillæ and deeper layers of epidermis. (Biesiadecki.)

a, Vascular papilla with capillary loop passing from subjacent vessel *c*; *b*, nerve papilla with tactile corpuscle, *t*. The latter exhibits transverse fibrous markings: three nerve-fibres, *d*, are represented as passing up to it: at *f f* these are seen in optical section.

(pp. 161 to 172). Many of the nerve-fibres, probably chiefly the non-medullated, are supplied to the plain muscular tissue of the minute hair-muscles, and to that of the blood-vessels.

NAILS AND HAIRS.

The nails and hairs are growths of the epidermis, agreeing essentially in nature with that membrane.

NAILS.

The posterior part of the nail, which is concealed in a groove of the skin is named its "root," the uncovered part is the "body," which

terminates in front by the "free edge." A small portion of the nail near the root, named from its shape the *lunula*, is whiter than the rest. This appearance is due partly to some degree of opacity of the substance of the nail at this point, and partly to the skin beneath being less vascular than in front.

The part of the corium to which the nail is attached, and by which in fact it is secreted or generated, is named the *matrix*. This portion of the skin is highly vascular and thickly covered with large vascular papillæ. Posteriorly the matrix forms a crescentic groove or fold, deep in the middle but getting shallower at the sides, which lodges the root of the nail; the rest of the matrix, before the groove, is usually named the *bed* of the nail. The small lighter coloured part of the matrix next the groove and corresponding with the lunula of the nail, is covered with papillæ having no regular arrangement, but the whole remaining surface of the matrix situated in front of this, and supporting the body of the nail, is marked with longitudinal and very slightly diverging ridges cleft at their summits into rows of papillæ. These ridges, or *laminæ*, as they are sometimes, and perhaps more suitably, named, fit

Fig. 225.

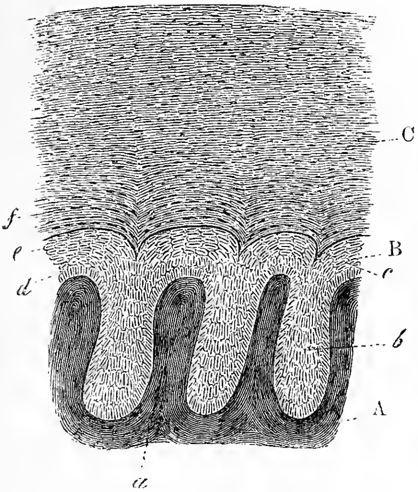


Fig. 225.—Vertical transverse section through a small portion of the nail and matrix, highly magnified (Kölliker).

A, corium of the nail-bed, raised into ridges or laminæ, *a*, fitting in between corresponding laminæ, *b*, of the nail; B, Malpighian, and C, horny layer; *d*, deepest and vertical cells; *e*, upper more flattened cells of Malpighian layer.

into corresponding furrows on the under surface of the nail. The cuticle, advancing from the dorsum of the finger and doubling back, becomes continuous with the nail near its posterior edge, that is, all round the margin of the groove in which the nail is lodged; in front the cuticle of the point of the finger becomes continuous with the under surface of the nail a little way behind its free edge.

The nail, like the cuticle, is made up of epithelial cells. The oldest and most superficial of these are the broadest and hardest, but at the same time very thin, and so intimately connected together that their respective limits are scarcely discernible. They form the exterior, horny part of the nail, and cohere together in irregular layers, so as to give this part a lamellar structure. On the other hand, the youngest cells, which are those situated at the root and under surface, are softer and of a rounded or polygonal shape. The deepest layer differs somewhat from the others, in having its cells elongated, and arranged perpendicularly, as in the case of the epidermis. Thus the under part of the nail (fig. 225, B) corresponds in nature with the Malpighian or mucous layer of

the epidermis, and the upper part (c) with the horny layer. As in the case of the epidermis, the hardened scales of the nails may be made to re-assume their cellular character by treatment with caustic alkali, and afterwards with water; and then it is seen that they still retain their nuclei.

The growth of the nail is effected by a constant generation of cells at the root and under surface. Each successive series of these cells being followed and pushed from their original place by others, they become flattened into dry, hard, and inseparably coherent scales. By the addition of new cells at the posterior edge the nail is made to advance, and by the apposition of similar particles to its under surface it grows in thickness; so that it is thicker at the free border than at the root. The nail being thus merely a modified and exuberant part of the epidermis, the question at one time raised, whether that membrane is continued underneath it, loses its significance. When a nail is thrown off by suppuration, or pulled away by violence, a new one is produced in its place, provided any of the cells of the deeper layers of the epithelium are left.

Formation and growth of the Nails.—In the third month of intra-uterine life the part of the embryonic corium which becomes the matrix of the nail is marked off by the commencing curvilinear groove, which limits it posteriorly and laterally. The epidermis on the matrix then begins to assume, in its under part, the characters of a nail, which may, therefore, be said to be at first embedded in the embryonic cuticle. The rudiment of the nail proper first appears at the posterior part of the matrix, and grows forward from this over the bed (Unna). After the end of the fifth month it becomes free at the anterior border, and in the seventh month decidedly begins and thenceforth continues to grow in length. At birth the free end is long and thin, being manifestly the earlier formed part which has been pushed forward. This breaks or is pared off after birth, and, as the infantile nail continues to grow, its flattened cells, at first easily separable, become harder and more coherent, as in after-life.

The average rate of growth of the nails is about $\frac{1}{32}$ of an inch per week. Berthold found that the nails grow rather faster in summer than in winter, and faster in the right hand than in the left. He also observed a difference in the nails of different fingers: thus the growth was fastest in the middle finger and slowest in the thumb. A careful series of experiments by H. J. Benham, have confirmed generally the observations of Berthold, but no clear difference could be observed between the two hands, and the growth appeared to be slowest in the little finger. In some individuals these differences were not observed.

HAIRS.

A hair consists of the root, which is fixed in the skin, the shaft or stem, and the point. The **stem** is generally cylindrical, but often more or less flattened: when the hair is entire, it becomes gradually smaller towards the point. The length and thickness vary greatly in different individuals and races of mankind as well as in different regions of the body. In the straight-haired races the individual hairs are coarser and thicker and the section more circular than in the woolly-haired races, in which the section is smaller and oval, the hairs being sometimes markedly flattened. The section is largest in the North American Indians, Chinese and especially in the Japanese. Light-coloured hair is usually finer than black.

The stem is covered with a coating of finely imbricated scales, the upwardly projecting edges of which give rise to a series of fine waved transverse lines, which may be seen with the microscope on the surface of the hair (fig. 226, A). Within this scaly covering, by some called

the *hair-cuticle*, is a *fibrous substance* which in all cases constitutes the chief part and often the whole of the stem; but in many hairs the axis is occupied by a substance of a different nature, called the *medulla* or *pith*. The *fibrous substance* is translucent, with short longitudinal opaque streaks of darker colour intermixed. It may be broken up into straight, rigid, longitudinal fibres, which, when separated, are found to be flattened, broad in the middle and pointed at each end, with dark and rough edges. The fibres again may be resolved into flattened cells of a fusiform outline; these are mostly transparent, or marked with only a few dark specks. The colour of the fibrous substance is caused by oblong patches of pigment-granules, and generally diffused colouring matter of less intensity. Very slender

Fig. 226.

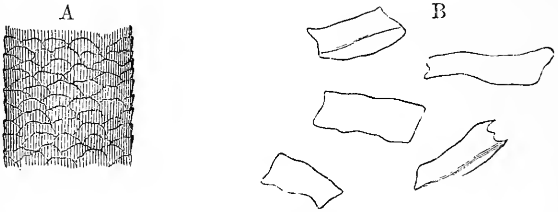


Fig. 226.—A, Surface of a white hair, magnified 160 diameters. The waved lines mark the upper or free edges of the cortical scales. B, Separated scales, magnified 350 diameter (after Kölliker).

elongated nuclei are also discovered by means of reagents, whilst specks or marks of another description in the fibrous substance are occasioned by minute irregularly shaped cavities containing air. These air-lacunules are abundant in white hairs, and are best seen in them, there being no risk of deception from pigment-specks; indeed they may be altogether wanting in very dark hairs. Viewed by transmitted light they are dark, but brilliantly white by reflected light. When a white hair has been boiled in water, ether, or oil of turpentine, these cavities become filled with fluid, and are then quite pellucid; but when a hair which has been thus treated is dried, the air quickly finds its way again into the lacunæ, and they resume their original aspect.

The *medulla* or *pith*, as already remarked, does not exist in all hairs. It is wanting in the fine hairs over the general surface of the body, and is not commonly met with in those of the head; nor in the hairs of children under five years. When present it occupies the centre of the shaft and ceases towards the point. When viewed by transmitted light, it is more opaque and deep-coloured than the fibrous part; by reflected light, on the other hand, it is white, its colour being chiefly due to the contained air-particles. It is composed of rows of soft cells, differing in shape, but generally angular, and containing minute particles, some resembling fine fat granules, intermixed with minute air-bubbles. The whole forms a continuous dark mass along the middle of the stem, interrupted at parts for a greater or less extent. In the latter case, the axis of the stem at the interruptions is fibrous like the surrounding parts.

The **root** of the hair is lighter in colour and softer than the stem; it swells out at its lower end into a bulbous enlargement or knob (fig.

227, *c*), and is received into a recess of the skin named the *hair-follicle*, which, when the hair is of considerable size, reaches down into the subcutaneous fat.

Fig. 227.

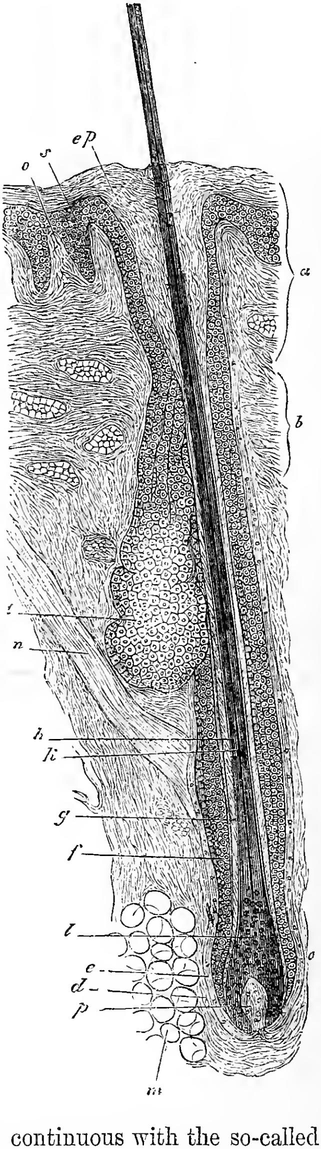


Fig. 227.—Hair-follicle, in longitudinal section. Moderately magnified. (Biesiadecki.)

a, mouth of the hair-follicle; *b*, its neck; *c*, lower bulbous enlargement; *d*, *e*, dermic coat (outer and inner layers, the innermost or hyaline layer is not shown); *f*, *g*, epidermic coat (outer and inner root-sheath); *h*, fibrous substance of the hair; *k*, medulla; *l*, hair-knob; *m*, fat in the subcutaneous tissue; *n*, arrector pili; *o*, papilla of the cutis; *p*, papilla of the hair-knob; *s*, Malpighian layer of the epidermis; *ep*, horny layer, represented in the figure as continuous with the inner root-sheath, but this is somewhat doubtful; *t*, sebaceous gland.

The follicle, which receives near its mouth the opening ducts of one or more sebaceous glands (*t*), is somewhat dilated at the bottom, to correspond with the bulging of the root; it consists of an outer coat continuous with the corium, and an epidermic lining continuous with the cuticle.

The outer or *dermic coat* of the follicle is thin but firm, and consists of three layers. The most external (fig. 229, *a*) is formed of connective tissue in longitudinal bundles, without elastic fibres, but with numerous corpuscles. It is highly vascular, and provided with nerves. It is continuous above with the corium, and determines the form of the follicle. The most internal layer (*hyaline layer*, Kölliker) (fig. 229, *d*) is a transparent homogeneous membrane, marked transversely on its inner surface with some raised lines, and not reaching so high as the mouth of the follicle; it corresponds with the membrana propria or basement membrane of allied structures. Between the two is a layer extending from the bottom of the follicle as high as the entrance of the sebaceous glands, composed of an indistinctly fibrous matrix, which tears transversely, and of transversely disposed connective tissue corpuscles, with oblong nuclei (fig. 229, *c*). This layer is continuous with the so-called papillary part of the cutis vera, and its blood-vessels are continuous above with those of that layer.

The *epidermic coat* of the follicle adheres closely to the root of the

hair, and commonly separates, in great part, from the follicle and abides by the hair when the latter is pulled out; hence it is sometimes named the "root-sheath." It consists of an outer, softer, and more opaque stratum (fig. 229, *e*), next to the dermic coat of the follicle, and an internal more transparent layer (fig. 229, *f*, *g*) next to the hair. The former, named also the *outer root-sheath*, and by much the thicker of the two, corresponds with the Malpighian layer of the epidermis in general, and contains soft polygonal cells, including pigment-granules in the

Fig. 228.

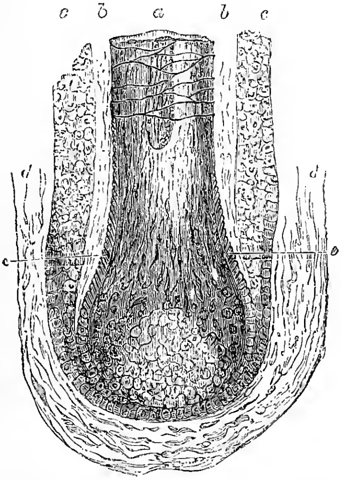


Fig. 229.

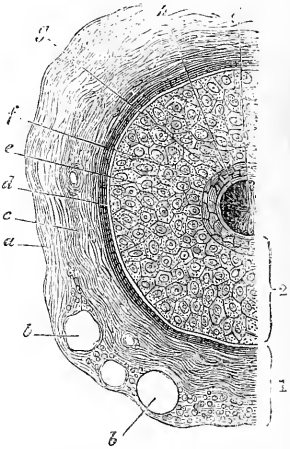


Fig. 228.—Magnified view of the bottom of a hair-follicle (after Kohlräusch).

a, hair showing medulla, fibrous substance, and cuticle; *b*, inner, and *c*, outer layer of the epidermic lining of the hair-follicle; *d*, dermic or external coat of the hair-follicle, shown in part; *e*, imbricated scales above forming a cortical layer on the surface of the hair. The adjacent cuticle of the root-sheath is not represented, and the papilla is only faintly indicated in the lower part of the knob.

Fig. 229.—Section of hair-follicle (Biesiadecki).

1, Dermic coat of follicle; 2, epidermic coat or root-sheath; *a*, outer layer of dermic coat, with blood-vessels, *b*, *b*, cut across; *c*, middle layer; *d*, inner or hyaline layer; *e*, outer root-sheath; *f*, *g*, inner root-sheath; *h*, cuticle of root-sheath; *i*, hair.

coloured races, which at the lower part form a much thinner stratum and pass continuously into those of the hair-knob; the internal layer or *inner root-sheath*, represents the superficial or horny layer of the epidermis, but is not continuous with that part of the skin, ceasing abruptly a little below the orifices of the sebaceous ducts. Lining the root-sheath internally is a layer of imbricated, downwardly projecting scales, the *cuticle of the root-sheath* (fig. 229, *h*), which is applied to the cuticle of the hair proper, to whose upwardly directed scales it fits like a mould. Its scales, as well as those of the hair-cuticle, pass, at the bottom of the follicle, into a layer of columnar cells which covers the surface of the hair-knob. The inner root-sheath itself consists of two layers, which towards the bottom of the follicle become blended into one. The innermost (that next the cuticula) is known as *Huxley's layer*; it consists of flattened polygonal nucleated cells, two or three deep. The outermost (*Henle's layer*) is composed of oblong, somewhat flattened cells without nuclei,

between which gaps frequently occur, so as to give it the aspect of a perforated membrane. At the lower part both layers pass into a single layer of large polygonal nucleated cells without openings between them. At the upper part also of the follicle the two layers of the inner root-sheath are not distinguishable from one another (Ebner).

The soft, bulbous enlargement of the root of the hair is attached by its base to the bottom of the follicle, and at the circumference of this attached part it is continuous with the epidermic lining (fig. 228). At the bottom of the follicle it, in fact, takes the place of the epidermis, of which it is a growth or extension, and this part of the follicle is the true matrix of the hair, being, in reality, a part of the corium

Fig. 230.

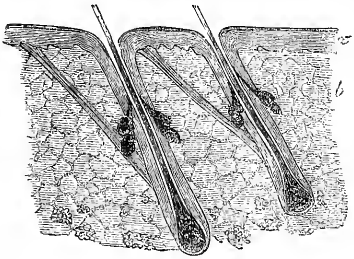


Fig. 230. SECTION OF THE SKIN OF THE HEAD, WITH TWO HAIR FOLLICLES, SLIGHTLY MAGNIFIED (Kölliker).

a, epidermis; *b*, corium; *c*, muscles of the hair-follicles.

(though sunk below the general surface), which supplies material for the production of the hair. From the bottom of this follicle rises a small vascular papilla, usually of a fungi-form shape (fig. 227, *p*). The papilla fits into a corresponding excavation of the hair-knob. In the large tactile hairs on the snout of the seal and some other animals it is very conspicuous. As the follicle, in short, is a recess of the corium, so the hair-papilla is a cutaneous papilla rising up in the bottom of it. Nervous branches enter the hair-follicles, but their final distribution is obscure. Some filaments enter the papilla, and many fibres appear to enter the epithelium, where they probably end as in the Malpighian layer of the epidermis. In the tactile hairs of animals, the nerves are described (Schöbl) as passing upwards over the outer root-sheath, there losing their white substance and forming a close plexus with vertical meshes; finally ending in an annular expansion, which encircles the hair just below the orifices of the sebaceous glands, and is in immediate connection with the hyaline layer of the follicle. In the larger tactile hairs the bulb is surrounded by cavernous tissue, which lies between the outer and middle layers of the dermic coat.

Muscles of the Hairs.—Slender bundles of plain muscular tissue (arrectores pili) are connected with the hair-follicles (figs. 227, 230). They arise, generally by a number of fasciculi, from the most superficial part of the corium, and joining to form a somewhat flattened and plexiform muscle they pass down obliquely to be inserted into the outside of the follicle below the sebaceous glands, which they in a measure embrace in their passage. In the dermic coat of the follicle some of the muscular fibres become transverse and partly encircle the lower part of the follicle. They are placed on the side to which the hair slopes, so that their action in elevating the hair is evident.

Development of hair in the fœtus.—The rudiments of the hairs may be discerned at the end of the third or beginning of the fourth month of intra-uterine life, as little black specks beneath the cuticle. They are formed of downgrowths of the Malpighian layer, which sink into the corium (fig. 231). A homogeneous limiting membrane next appears (*i*), inclosing the collection of

cells, and continuous above with a similar simple film which at this time lies between the cuticle and the corium ; it becomes the innermost or hyaline layer of the dermic coat of the follicle. The hair-rudiments next lengthen and swell out at the bottom, so as to assume a flask-shape. Outside the limitary membrane, the fibres, corpuscles, and other constituents of the dermic coat of the follicle become formed. While this is going on outside, the cells within the follicle undergo changes. Those in the middle lengthen out conformably with the axis of the follicle, and give rise to the appearance of a short conical miniature hair, faintly distinguishable

Fig. 231.

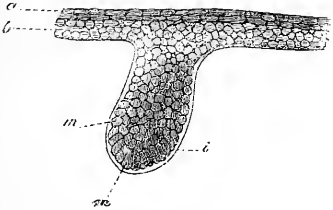


Fig. 231.—Hair-rudiment from an embryo of six weeks, magnified 350 diameters (Kölliker).

a, horny, and *b*, mucous or Malpighian layer of cuticle ; *i*, limitary membrane ; *m*, cells (some of which are assuming an oblong figure) which chiefly form the future hair

by difference of shade from the surrounding mass of cells, which are also slightly elongated, but across the direction of the follicle. The papilla (fig. 232, *h*) grows up from the corium into the swollen root of the little hair ; and the residuary cells contained within the rudimentary follicle form the root-sheath, the inner

Fig. 232.

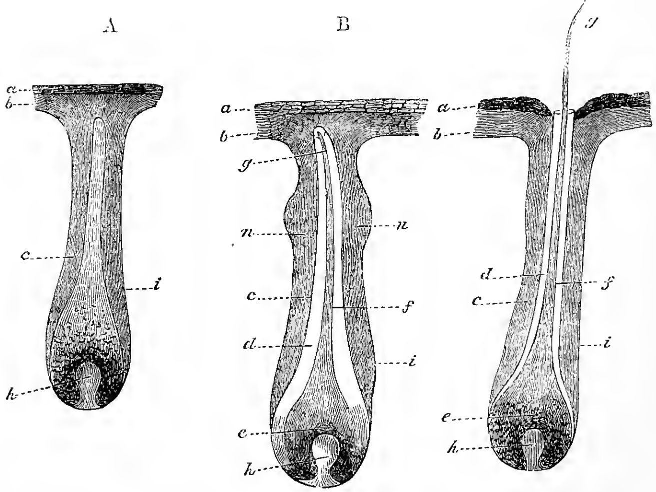


Fig. 232.—A. Rudiment of a hair of the eyebrow, magnified 50 diameters (Kölliker).

The cells form an internal cone indicating the position of the future hair. *a*, horny layer of cuticle ; *b*, mucous layer ; *c*, external layer of root-sheath ; *i*, limitary membrane ; *h*, papilla.

B.—Hair-rudiment from the eyebrow, with the young hair not yet risen through the cuticle.

e, hair-knob ; *f*, stem, and *g*, point of the hair ; *d*, internal layer of the root-sheath, still inclosing the hair ; *n*, *n*, commencing sebaceous follicles.

C.—Hair-follicle from the eyebrow with the hair just protruded ; the inner layer of the root-sheath rises to the mouth of the hair-follicle.

layer of which, or inner root sheath, lying next to the hair (fig. 232, *d*), is soon distinguished by its translucency from the more opaque outer part that fills up the rest of the cavity. The young hair continuing to grow, at last perforates the cuticle (fig. 232, C, *g*), either directly or after first slanting up for some way between the mucous and horny strata : it is often bent like a whip, and then the doubled part protrudes.

The first hairs produced constitute the *lanugo;* their eruption takes place about the fifth month of intra-uterine life, but some of them are shed before birth, and are found floating in the liquor amnii.

According to Kölliker's observations, the infantile hairs are entirely shed and renewed within a few months after birth ; those of the general surface first, and afterwards the hairs of the eyelashes and head, which he finds in process of change in infants about a year old. The new hairs are generated in the follicles of the old (fig. 233). An increased growth of cells takes glace in the soft hair-knob, and

Fig. 233.

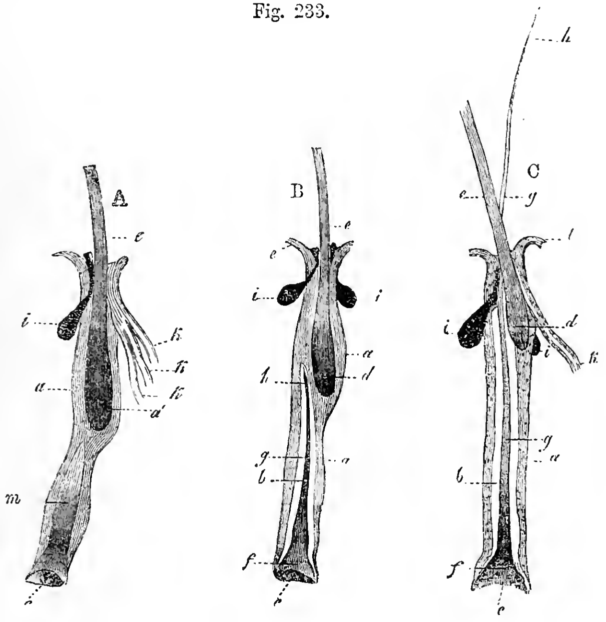


Fig. 233.—EYELASHES OF AN INFANT, PULLED OUT FROM THEIR FOLLICLES, MAGNIFIED 20 DIAMETERS (Kölliker).

A, the new cell-growth forming a cone, *m*, in the interior (as in fig. 232, A). In B, the cone has separated into the new hair, *f*, *g*, and its inner root-sheath, *b* ; *a*, outer root-sheath of new hair ; *c*, pit for papilla ; *d* and *e*, the knob and stem of old hair ; *f*, knob ; *g*, stem ; and *h*, the point of new hair ; *i*, sebaceous glands ; *k*, *k*, sweat-glands here opening into the mouth of the hair-follicle. C, eyelash with young hair come forth, *l*, epidermis continuous with outer root-sheath ; other letters as in preceding figures.

in the adjoining part of the root-sheath (the outer layer) : the growing mass seems to push up the hair-knob, and detach it from its generative papilla. The newly-formed mass of cells occupying the lower part of the follicle, and resting on the papilla, is gradually converted into a new hair with its root-sheath, just as in the primitive process of formation in the embryo ; and as the new hair lengthens and emerges from the follicle, the old one, separated from its matrix by the interposition of the new growth, is gradually pushed towards the opening, and at last falls out, its root-sheath having previously undergone partial absorption. According to most observers the new hair (when the hairs are changed) does not grow from

the old papilla, but is formed in a fresh hair-germ which buds out from the outer root-sheath, and in which a new papilla becomes developed; the old papilla and hair-bulb and the lower part of the primary follicle having first become gradually atrophied. When a hair is pulled out, a new one grows in its place, provided the follicle (from which the growth proceeds) remains entire.

Growth of hair.—On the surface of the papilla, at the bottom of the follicle, there is a continual multiplication of cells. These for the most part lengthen out and unite into the flattened fibres which compose the fibrous part of the hair, and certain of them getting filled with pigment, give rise to the coloured streaks and patches in that tissue; their nuclei, at first, also lengthen in the same manner, but, at last, partly become indistinct. The cells next the circumference expand into the scales which form the imbricated cuticular layer. The medulla, where it exists, is formed by the cells nearest the centre.

The substance of the hair, of epidermic nature, is, like the epidermis itself, quite extravascular, but like that structure also, it is organised and subject to internal organic changes. Thus, in the progress of its growth, the cells change their figure, and acquire greater consistency. In consequence of their elongation, the hair, bulbous at the commencement, becomes reduced in diameter, and cylindrical above. But it cannot be said to what precise distance from the root organic changes may extend. Some have imagined that the hairs are slowly permeated by a fluid from the root to the point, but this has not been proved. The sudden change of the colour of the hair from dark to grey, which sometimes happens, has never been satisfactorily explained: it appears generally to be due to the development of air between the elongated cells composing the hair.

The rate of growth of hair is about half-an-inch per month.

Distribution and arrangement.—Hairs are found on all parts of the skin except the palms of the hands and soles of the feet, the dorsal surface of the third phalanges of the fingers and toes, the glans, and the inner surface of the prepuce. On the scalp they are set in groups, on the rest of the skin for the most part singly. Except those of the eyelashes, which are implanted perpendicularly to the surface, they have usually a slanting direction, which is constant in the same parts. In the negro the hair follicles have been found to be curved, so that the papilla may look in a direction parallel to or even away from the surface of the skin (Stewart).

With the exception of the bones and teeth, no tissue of the body withstands decay after death so long as the hair, and hence it is often found preserved in sepulchres, when nothing else remains but the skeleton.

GLANDS OF THE SKIN.

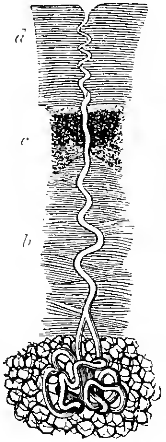
The sudoriferous glands or sweat-glands (figs. 221 and 234).—These are seated on the under surface of the corium, and at variable depths in the subcutaneous adipose tissue. They have the appearance of small round reddish bodies, each of which, when examined with the microscope, is found to consist of a fine tube, coiled up into a ball (though sometimes forming an irregular or flattened figure); from which the tube is continued, as the duct of the gland, upwards through the true skin and cuticle, and opens on the surface by a slightly widened orifice. The duct, as it passes through the epidermis, is twisted like a corkscrew, that is, in parts where the epidermis is sufficiently thick to give room for this; lower down it is straight or but slightly curved. Sometimes the duct is formed of two coiled-up branches which join at a short distance from the gland, as in fig. 234. The tube, both in the gland and where it forms the excretory duct, has an investment of connective tissue, continuous with the corium, and reaching no higher than the surface of the true skin, and within this consists of a thin membrana propria and an epithelial lining, consisting in the gland of a single layer

of cubical or columnar cells (often containing brownish pigment) and, in the duct, of two or more layers bounded next the lumen by a fine cuticular lining. The epithelium of the duct is continuous with the epidermis, which alone forms the twisted part of the duct. The tube is larger in the proper secreting portion of the gland than in the duct, and in the former,

Fig. 234.—Magnified view of a sweat-gland, with its duct (Wagner).

a, the gland surrounded by fat-cells; *b*, the duct passing through the corium; *c*, its continuation through the lower, and *d*, through the upper part of the epidermis.

Fig. 234.

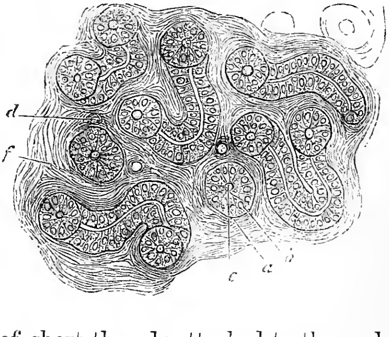


between the epithelium and the basement membrane, is a layer of plain muscular fibres longitudinally disposed. These are absent in the duct, which is itself often coiled two or three times before leaving the gland, but its coils are distinguished from those of the gland proper by the differences just mentioned. The secreting cells of the sweat-glands show the peculiar rod-like structure characteristic of many gland-cells, and minute canals are said to pass from the lumen of the tube between the opposed surfaces of the cells (Ranvier). In the large glands in the axilla, at the root of the penis, on the labia majora, and in the neighbourhood of the anus, the layer of non-striated muscular fibre-cells between the epithelium and basement membrane is very well marked. In the larger glands, also, the duct is rarely simple, being more usually parted by repeated dichotomous division into several branches, which before ending give off short cæcal processes; in rare cases the branches anastomose. On carefully detaching the cuticle from the true skin, after its connection

Fig. 235. — Section of a sweat-gland. Highly magnified (Biesiadecki).

The tubules are seen variously cut. *a*, basement-membrane; *b*, lining cells; *c*, lumen of tube; *d*, blood-vessels and uniting connective tissue.

Fig. 235.



has been loosened by putrefaction, it usually happens that the cuticular linings of the sweat-ducts get separated from their interior to a certain depth, and are drawn out in form of short threads attached to the under surface of the epidermis. The coils of the gland-tube are loosely held together by connective tissue (fig. 235), which may form a sort of capsule round the body of the gland. Each little sweat-gland is supplied with a dense cluster of capillary blood-vessels.

Distribution.—Sweat-glands exist most numerously in regions unprovided with hairs, but they occur in all parts of the skin, and may in some cases

open into hair-follicles. According to Krause, nearly 2800 open on a square inch of the palm of the hand, and somewhat fewer on an equal extent of the sole of the foot. He assigns rather more than half this number to a square inch on the back of the hand, and not quite so many to an equal portion of surface on the forehead, and the front and sides of the neck. On the breast, abdomen, and fore-arm, he reckons about 1100 to the inch, while on the lower limbs and the back part of the neck and trunk, the number in the same space is not more than from 400 to 600.

The size of the sweat-glands also varies. According to the observer last named, their average diameter is about $\frac{1}{70}$ of an inch; but in some parts they are larger than this—as, for example, in the groin, but especially in the axilla. In this last situation Krause found the greater number to measure from $\frac{1}{36}$ to $\frac{1}{12}$ of an inch, and some nearly $\frac{1}{6}$ of an inch in diameter.

The **development** of the sweat-glands has been carefully studied by Kölliker. Their rudiments, when first discoverable in the embryo, have much the same

Fig. 236.

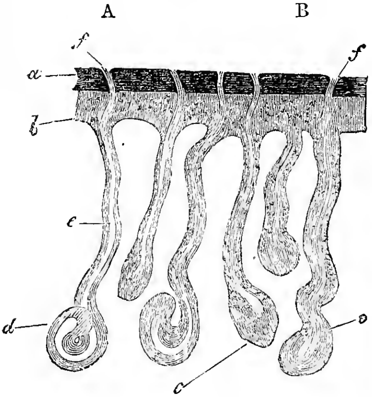


Fig. 237.

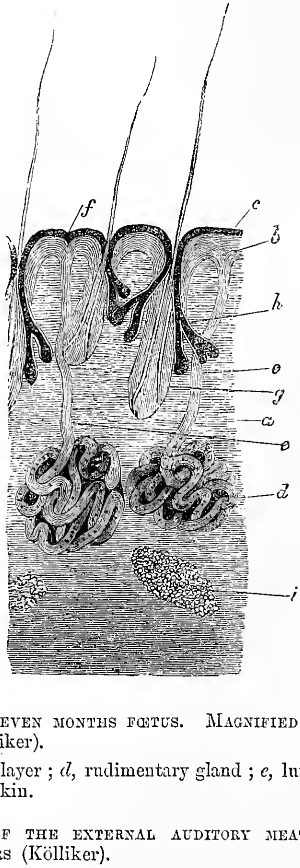


Fig. 236.—Developing sweat glands from a seven months fœtus. Magnified 50 diameters (Kölliker).

a, horny layer of the epidermis ; *b*, Malpighian layer ; *d*, rudimentary gland ; *e*, lumen of the duct, opening at *f* upon the surface of the skin.

Fig. 237.—Ceruminous glands in the skin of the external auditory meatus Magnified 20 diameters (Kölliker).

a, cutis vera ; *b*, Malpighian layer, *c*, horny layer of the epidermis ; *d*, glandular coil ; *e*, duct ; *f*, its opening ; *g*, hair follicle ; *h*, sebaceous gland ; *i*, fat.

appearance as those of the hairs, and, in like manner, consist of processes of the mucous layer of the epidermis, which pass down and are received into corresponding recesses of the corium (fig. 236). They are formed throughout of cells collected into a solid mass of a club shape, continuous by its small end with the Malpighian layer of the cuticle, and elsewhere surrounded by a homogeneous limiting membrane, which is prolonged above between the corium and cuticle. The subsequent changes consist in the elongation of the rudimentary gland, the formation of a cavity along its axis—at first without an outlet—the prolongation of its canal through the epidermis to open on the surface, and, in the meantime, the coiling up of the gradually lengthening gland-tube into a compact ball, and the twisting of the excretory duct as it proceeds to the orifice. The plain muscular tissue of the sweat-glands is said to be developed from some of the epithelium-cells of the rudimentary gland (Ranvier). If this be so, it is the only known instance, in the higher animals, of muscular tissue being developed from the ectoderm.

The ceruminous glands in the auditory passage consist of a tube coiled into a ball, like the sweat-glands (fig. 237): and there is such a further correspondence between the two, in structure and mode of development, that the ceruminous glands may be regarded as a mere variety of the sudoriferous.

Fig. 238.

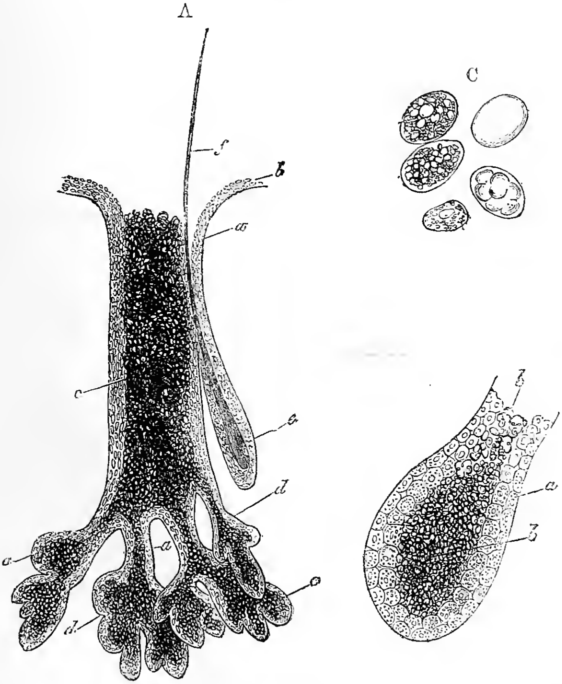


Fig. 238.—A, Sebaceous gland from the nose with branched duct, attached to a small hair-follicle. Magnified 50 diameters (from Kölliker).

a, epithelium continuous with *b*, the Malpighian layer of the epidermis ; *c*, contents of gland ; *d*, *d*, the groups of saccules on the branches of the duct ; *e*, hair-follicle ; *f*, hair.

B, Terminal saccule of a sebaceous gland. Magnified 250 diameters.

a, epithelium lining the saccule ; *b*, sebaceous matter, partly still within the cells.

C, Separated cells from the interior of an alveolus, containing fatty particles of varying degrees of fineness (from Kölliker).

The **sebaceous glands** (figs. 227, 238, A) pour out their secretion at the roots of the hairs, for, with very few exceptions, they open into the hair-follicles, and are found wherever there are hairs. Each has a short duct, which opens at a little distance within the mouth of the hair-follicle, and by its other end, leads to a cluster of small rounded secreting saccules, which as well as the duct are lined by epithelium (fig. 238, B), and usually charged with the fatty secretion, mixed with detached epithelium-particles. The number of saccular recesses connected with the duct usually varies from four or five to twenty; it may be reduced to two or three, in very small glands, or even to one, but this is rare. These glands are lodged in the substance of the corium. Several may open into the same hair-follicle, surrounding it on all sides, and their size is not regulated by the magnitude of the hair. Thus, some of the largest are connected with the fine downy hairs on the alæ of the nose and other parts of the face, and there they often become unduly charged with pent-up secretion.

Development of the sebaceous glands.—The rudiments of the sebaceous glands sprout like little buds from the sides of the hair-follicles; they are at first, in fact, excrescences of the external layer of the root-sheath (fig. 239), and are composed entirely of similar cells. Each little process soon assumes a flask-shape and in due time a group of cells containing fat particles appears in its centre, and gradually extends itself along the axis of the pedicle until it penetrates through the root-sheath, and the fat-cells thus escape into the cavity of the hair-follicle, and constitute the first secretion of the sebaceous gland. They are soon succeeded by others of the same kind, and the little gland is established in its office. Additional saccules and recesses, by which the originally simple cavity of the gland is complicated, are formed by budding out of its epithelium, as the first was produced from the epithelial root-sheath, and are excavated in a similar manner.

Fig. 239.

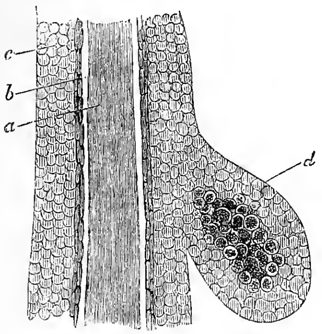


Fig. 239.—Development of a sebaceous gland in a six months' fœtus. 250 diameters (Kölliker).

a, hair; *b*, inner root-sheath; *c*, outer root-sheath of hair-follicle; *d*, rudiment of sebaceous gland.

It would thus appear that the rudiments of the hair-follicles, sweat-glands, and sebaceous glands, are all derived from the same source. They all originally appear as solid bud-like excrescences of the soft Malpighian or mucous layer of the epidermis, (for the outer stratum of the root-sheath must be regarded as such); these grow down into the corium, in which recesses are formed to receive them, and which, of course, yields the material required both for the production of new cells, for their further growth, and for the maintenance of their secreting function.

Recent Literature:—On the skin generally. *J. Neumann*, Verbreit. d. organ. Muskeln &c. Allg. Wien. Med. Zeitung, 1868; *Biesiadecki*, Article, "Skin" in Stricker's Handbook, 1871; *Tomsa*, in Arch. f. Dermat., 1873; *Langerhans*, Ue. Tastk. u. rete. Malp., Arch. f. mikr. Anat., 1873; *Stirling*, (cutis of dog) in Journ. of Anat. and Phys., 1875; *Unna*, Oberhaut u. ihrer Anhangsg., Arch. f. mikr. Anat., 1876; *Remy*, in Journ. de l'anat., 1878; *Ranvier*, in Compt. rend., 1879.

On the hairs or nails especially. *Pfaff*, Das menschliche Haar. &c., 1866; *Götte*, in Arch. f. mikr. Anat., 1868; *Dietl*, in Wiener Sitzungsb., 1871–1873; *Stieda*, in Arch. f.

mikr. Anat. 1872, 1873; *Schöbl*, in the same Journal (tactile hairs); *Stewart*, On the scalp of a negro, Monthly micr. Journal, 1873; *Heynold*, in Virch. Arch., 1875, 1876; *Schulin*, in Marb. Sitzungsb., 1876, and in Zeitschr. f. Anat. u. Entw., 1877; *Ebner*, in Wiener Sitzungsb., 1876; *Esoff*, in Virch. Arch., 1877; *Loewe*, in Arch. f. mikr. Anat., 1878.

On the glands of the skin, *Sappey*, in Gaz. méd., 1863; *Heynold*, in Virch. Arch., 1874; *Hörschelmann*, Dissert., Dorpat, 1875; *Hesse*, in Zeitschr. f. Anat. u. Entw., 1876; *Sangster*, in the Quart. J. of micr. Sci., 1877; *Ranvier*, in Comptes rend., LXXXIX., 1879.

On the lymphatics, *J. Neumann*, "Zur Kenntn. d. Lymphg. d. Haut," Vienna, 1873; *Hoggan*, in the Journ. de l'anat., 1879; *Klein*, in Quart. Journ. of micr. Sci., 1881; *Key and Retzius*, in Biologische Unters., Stockholm, 1881.

On the nerves of the skin, *Langerhans*, in Virch. Arch., 1868; *Eberth*, in Arch. f. mikr. Anat., VI., 1870; *Paladino*, in Bull. d. assoc. d. natur. di Napoli, 1871; *Merkel*, in Arch. f. mikr. Anat., XI.; *Arnstein*, in Wiener Sitzungsb., 1876; *Bonnet*, in Morph. Jahrb. IV., 1878 (nerves of hair-follicles and lit.); *Ranvier*, in the Quart. J. of micr. Sci., 1880; *Möisisowicz*, in Wiener Sitzungsb., LXXI., 1876.

ADDENDA.

A few additional remarks may here be made concerning some of the subjects treated of in the preceding part on General Anatomy, chiefly on account of additional light having been thrown on them by researches which have been published since the previous sheets were printed.

The structure and mode of division of the cell-nucleus.* It has been shown that in addition to the evident network within the nucleus which was previously described (p. 9, fig. 8), there frequently exists a far finer interlacement of exquisitely delicate fibrils of nucleoplasm which occupy the meshes of the coarse network, and except with the best immersion objectives, either remain unseen, or their nodal points appear in the form of fine granules (as in fig. 10, *a*, p. 12). It was the staining of this finest network which led to the notion that the nuclear matrix itself in the resting cell is slightly stained by hæmatoxylin or safranin (see p. 9), and therefore contains "chromatic" substance in solution; probably however this is not the case.†

A marked difference between the active and the resting nucleus consists in the fact that in the former the nucleoplasmic fibres, at any one stage of division, are of uniform size, while in the resting condition they show great irregularities, being in some parts comparatively coarse and in others immeasurably fine. This difference is still further accentuated by the accumulation of the nucleoplasm in the resting nucleus at one or more of the nodes of the network into irregular or rounded clumps, the latter being the nucleoli. In a nucleus which is about to undergo division and in new nuclei which have just been formed by division (fig 10, *q*) not only are the nucleoplasmic filaments uniform but there are no nodal clumps or nucleoli; so that the presence of the last named bodies may be said to be characteristic of a resting condition of the nucleus. Indeed in the completely inactive condition it may happen that the nucleoplasm becomes wholly collected to form nuclear membrane and nucleolus, so that the network is either no longer present or has become so highly attenuated as to be no longer discernible.

The longitudinal cleavage of the V-shaped fibres in the aster-phase (p. 13 and fig. 10, *g*, *h*) is said by Retzius to occur constantly, so that in this way the number of those filaments is doubled. It is not improbable that the two fibres resulting from the cleavage pass into different daughter-nuclei, but it has not been possible to trace this with sufficient clearness.

The very widely diffused occurrence of the phenomena of karyokinesis (it has now been observed in almost every description of active cell in the animal body)

* *Klein*, Atlas of Histology; *Fleming*, Beiträge, &c., No. III, in Arch. f. mikr. Anat., XX., 1881; *Pfitzner*, Beobachtungen, &c., in the same Journal; *Retzius*, Biologische Untersuch., Stockholm, 1881.

† According to Klein these fibrils of the nucleus are directly continuous with the protoplasmic intracellular reticulum; but this is doubted by other observers, who describe the nucleus as being sharply bounded from the surrounding protoplasm.

has led most observers to the conclusion that it is an essential preliminary to cell-division. Some however, still believe that in some cases, simple constriction of the nucleus into two, or its budding into several, may suffice to produce division, it being thought that the time occupied in the complex process of karyokinesis is too long to permit of the active cell-multiplication which is known to occur in certain cases. As a fact, however, the time occupied is not so long as might be supposed :—in cold-blooded animals it has been found to take from one and a half to five hours; in cells from a carcinoma in man only half an hour (Fleming); and in cells of the intervertebral cartilage of the cat, examined in warm salt solution, the process of karyokinesis was on one occasion observed by me to proceed to the stage of the formation of the daughter-nuclei (amphi-astral stage) in a few minutes (E. A. S.).

Fig. 240.

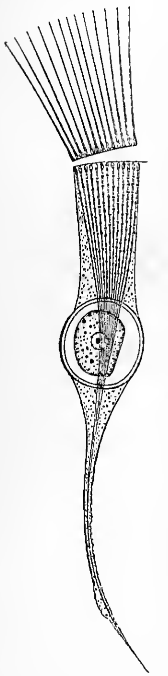


Fig. 240.—A CILIATED EPITHELIUM-CELL OF A MOLLUSK (Engelmann).

Lastly, Fleming has conclusively shown that in the dividing nucleus of the plant-cell and in that of the animal ovum (see p. 14), the chromatic substance is also in the form of filaments, although these are so small that they can only be made out by the most improved objectives.

Ciliated Epithelium.—It has been shown by Engelmann * that in large ciliated cells such as those which line the alimentary canal of some mollusks, e. g. the mussel and oyster, it is possible to make out that the highly refracting free border of the cell to which the cilia are attached is in reality formed of a number of small juxtaposed fusiform or cylindrical knobs (*basal pieces*). To each of these a cilium is attached on the one side, and from the other end there passes towards the end of the cell a fine, varicose filament; these filaments are termed by Engelmann the *rootlets* of the cilia. They approach one another as they traverse the length of the cell, and may be united towards the extremity into a single thread. They are not connected with the nucleus. The cilia are attached to the basal pieces of the cell, each one by a somewhat narrow, soft portion or neck (*intermediate segment* of Engelmann). It is here that the cilia usually break off from the cell (see fig. 240). Beyond the neck the cilium swells out into a small bulbous enlargement, and from this the shaft tapers gradually to its extremity. The rootlets, as well as the cilia themselves, are said by Engelmann to be double refracting, whereas the basal piece is isotropous. A similar structure, although less distinct, is also to be made out in ciliated cells from the higher animals (frog and rabbit).

Striated muscular fibre.—There is good reason to believe from its chemical reactions that the sarcolemma is of the nature of connective tissue, and not a cell-membrane as has generally been thought.† The intimate nature of its union with the tendon-bundle (see fig. 127, p. 130) would seem to point to the same conclusion.

The ending of sensory nerves.—Many of the nerve-fibres of those parts of the skin which are especially endowed with tactile sensibility, penetrate into the epithelium and terminate after branching a number of times, in expansions of the axis-cylinder (*tactile menisci*) which are applied to certain cells of the deeper layers of the epidermis. These cells are apparently those described as tactile cells by Merkel (see p. 137), but according to Ranvier ‡ there is no actual connection of the nerve-fibre with the cell.

* Pflüger's Archiv. XXIII., 1880.

† *Froriep*, in the Arch. f. Anat., 1878. See also on the subject of striated muscle a paper by *Merkel* (in the Arch. f. mikr. Anat., XIX., 1881), who somewhat modifies the view he had before taken (see p. 128), and another by *Retzius* (Biol. Unters., 1881), who describes the appearances of the muscle of Dytiscus much in the same manner as was done by me (Phil. Trans., 1873), but gives a different interpretation of them (E.A.S.).

‡ Nouvelles recherches s. l. corp. du tact, Comptes rendus, 1880; and Traité technique, sixième fascicule, 1882.

16 weeks. 30 pp. a week

SPLANCHNOLOGY.

THE CEREBRO-SPINAL AXIS.

The *cerebro-spinal axis* is divided by anatomists into the *brain* or *encephalon*, the enlarged upper mass placed within the cranium, and the *spinal cord* contained within the vertebral canal. It is symmetrical in its form and structure throughout, consisting of a right and a left half, separated to a certain extent by longitudinal fissures, but united by various portions of white and grey nervous substance which cross from one side to the other, and form the *commissures* of the brain and spinal cord.

The cerebro-spinal axis is surrounded within the skull and vertebral canal by three connective tissue membranes, between which are spaces occupied by a clear fluid similar in its general nature to lymph (cerebro-spinal fluid). These envelopes, which will be described hereafter, are, 1st, a firm fibrous membrane named the dura mater, which is placed most superficially; 2nd, a delicate membrane called the arachnoid; and, 3rd, a highly vascular membrane named the pia mater, which is next to, and closely invests the surface of the brain and cord.

SPINAL CORD.

The **spinal cord,** or **spinal marrow** (medulla spinalis), is that part of the cerebro-spinal axis which is situated within the vertebral canal. It is about 18 inches (45 centim.) long, and extends from the margin of the foramen magnum of the occipital bone to about the lower part of the body of the first lumbar vertebra. Above, it is continued into the medulla oblongata; below, it tapers conically and ends in a slender filament, the *filum terminale* or *central ligament* of the spinal cord.

Although the cord usually ends near the lower border of the body of the first lumbar vertebra, its termination is sometimes a little above or below that point, as opposite to the last dorsal or to the second lumbar vertebra. The position of the lower end of the cord also varies according to the state of curvature of the vertebral column, in the flexion forwards of which the end of the cord is slightly raised. In the fœtus, at an early period, the embryonic cord occupies the whole length of the vertebral canal; but, after the third month, the canal and the roots of the lumbar and sacral nerves begin to grow more rapidly than the cord itself, so that at birth the lower end reaches only to the third lumbar vertebra.

The cord is enclosed in the vertebral canal within a sheath (theca, figs. 241, 244) considerably longer and larger than itself, formed by the dura mater, and separated from the walls of the canal by venous plexuses,

and much loose areolar tissue. The cavity of the theca between the pia mater and the dura mater is occupied by cerebro-spinal fluid, and is divided by the curtain-like arachnoid into the two spaces, subdural and subarachnoid, above mentioned. Within the latter the cord, covered

Fig. 241.

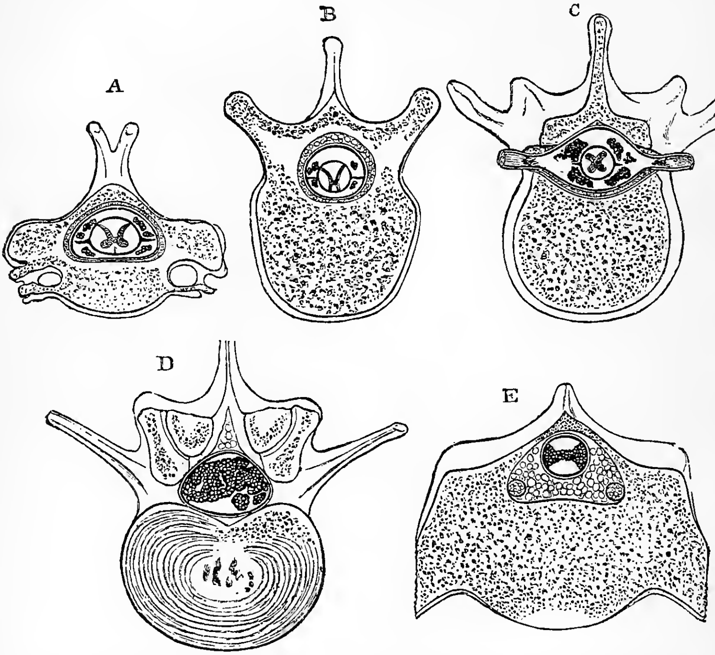


Fig. 241.—Sections showing the general relations of the spinal cord to the inclosing theca, and of this to the vertebral canal (Key and Retzius).

A, through the fifth cervical vertebra; B, through the tenth dorsal vertebra; C, through the first lumbar vertebra and the foramen of exit of the twelfth dorsal nerve-roots; D, through the disk between the second and third lumbar vertebræ; E, through the first sacral vertebra. In A, B, and C, the cord, covered by pia mater, is seen in the centre, with the ligamentum denticulatum attached to it on either side; the nerve-roots on either side form small groups which, since they pass obliquely downwards to their foramina of exit, are cut across; the dura matral sheath is separated by a considerable space from the cord, and by a quantity of loose areolar and fatty tissue from the wall of the vertebral canal. This tissue is in smaller amount in C. D and E are below the termination of the cord, and show sections of the nerve-bundles of the cauda equina within the theca, which is very large in D, but comparatively small in E, the vertebral canal in the latter being largely occupied by adipose tissue. In this are seen the sections of two large veins. The arachnoid is not represented in any of these sections.

closely by pia mater, is suspended, being kept in position by a ligament on each side (ligamentum denticulatum), which fixes it at frequent intervals to its sheath, and by the roots of the spinal nerves which pass across the space from the surface of the cord towards the intervertebral foramina.

The uppermost nerve-roots cross the space nearly horizontally

(fig. 244 A), but the rest below the first one or two pass across with a more and more oblique downward inclination until their direction is almost vertical (fig. 244 B), and indeed the lower part of the theca below the termination of the cord (fig. 241, D, E), is occupied by the descending roots of the lumbar and sacral nerves, passing to the foramina between the corresponding vertebræ. The mass of nerve-roots, which conceals the delicate filum terminale, is named the *cauda equina* (fig. 244 C).

Fig. 242.

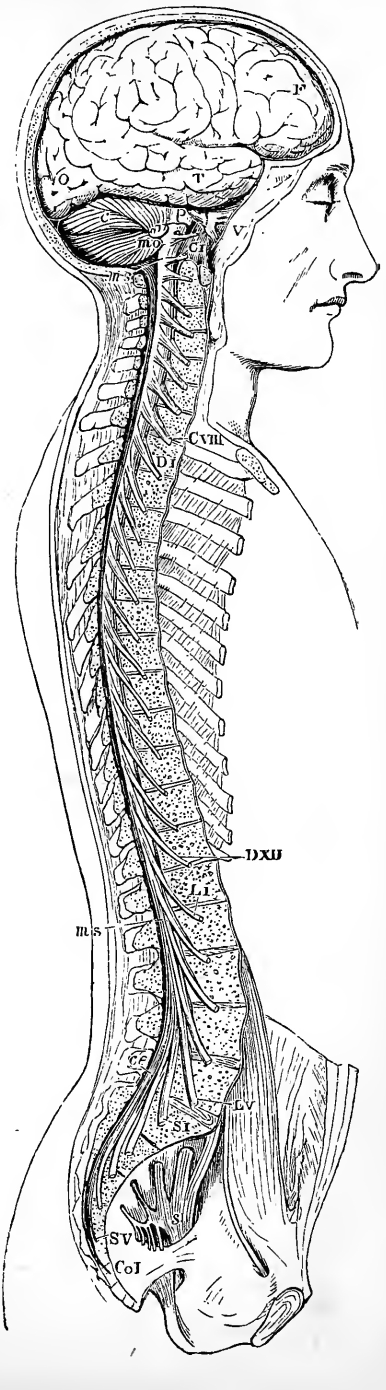


Fig. 242.—View of the cerebro-spinal axis (after Bourgery). $\frac{1}{5}$

The right half of the cranium and trunk of the body has been removed by a vertical section; the membranes of the right side of the brain and spinal cord have been cleared away, and the roots and first part of the fifth and ninth cranial nerves, and of all the spinal nerves of the right side, have been dissected out and laid separately on the wall of the skull and on the several vertebræ opposite to the place of their natural exit from the cranio-spinal cavity.

F, T, O, cerebrum; C, cerebellum; P, pons Varolii; *m o*, medulla oblongata; *m s*, *m s*, point to the upper and lower extremities of the spinal marrow; *c e*, on the last lumbar vertebral spine, marks the cauda equina; v, the three principal branches of the nervus trigeminus; C I, the sub-occipital or first cervical nerve; C VIII, the eighth or lowest cervical nerve; D I, the first dorsal nerve; D XII, the last dorsal; L I, the first lumbar nerve; L V, the last lumbar; S I, the first sacral nerve; S V, the fifth; Co I, the coccygeal nerve; *s*, the left sacral plexus.*

* The relation between the bodies and spines of the vertebræ and the places of attachment of the nerve-roots to the cord is also illustrated by this figure. For more detailed information on this point the reader may consult Gowers "The Diagnosis of Diseases of the Spinal Cord," 1880.

Fig. 243.

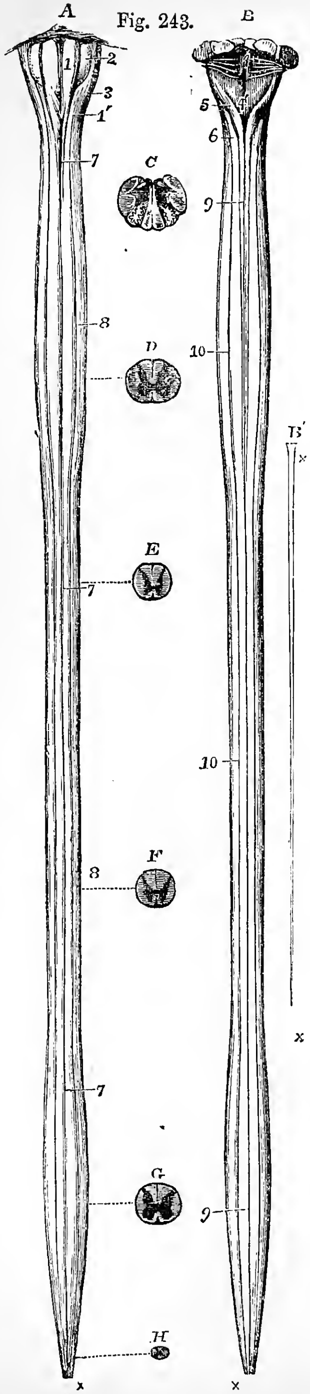


Fig. 243.—Anterior and posterior views of the medulla oblongata and spinal cord with sections (Allen Thomson). ½

The cord has been divested of its membranes and of the roots of the nerves. A is an anterior, B a posterior view. In these figures the filiform prolongation, represented separately in B′, has been removed; C shows a transverse section through the middle of the medulla oblongata; D, a section through the middle of the cervical enlargement of the cord; E, through the upper dorsal region; F, through the lower; G, through the middle of the lumbar enlargement; and H, near the lower end of the conus medullaris.

1 to 6 refer to parts of the medulla oblongata; the remaining numbers to parts of the spinal cord.

1, pyramids; 1′, their decussation; 2, olivary bodies; 3, lateral columns; 4, posterior surface of the medulla oblongata; 4′, calamus scriptorius; 5, funiculus gracilis; 6, posterior lateral columns passing to the side; 7, 7, anterior median fissure of the spinal cord; 8, 8, antero-lateral impression corresponding to the attachments of the anterior nerve roots; 9, 9, posterior median fissure; 10, 10, postero-lateral groove; ×, tapering extremity of the cord; ×, ×, in B′, filum terminale.

In section the cord is nearly circular, especially in the dorsal region, but it is somewhat flattened before and behind. In the dorsal region, it measures about ten millimeters from side to side, and about eight from before back. The cord is not, however, of uniform diameter throughout, but is swollen out in the cervical and lower dorsal regions, two enlargements being thereby produced—an upper or cervical, and a lower or lumbar (fig. 243). Of these the cervical enlargement is of greater size and extent than the lumbar. It extends from the upper limit of the cord to the first or second dorsal vertebra; it is largest opposite the fifth or sixth cervical vertebra, where it measures from 13 to 14 mm. from side to side. The lower or lumbar enlargement begins at the tenth dorsal vertebra, is largest opposite the twelfth dorsal (11—13 mm. across), and from this point becomes gradually smaller; its antero-posterior diameter is more nearly equal to the transverse than is the case in the cervical enlargement. Below

the lumbar enlargement the cord tapers in the form of a cone (*conus medullaris*), from the apex of which the small filiform prolongation is continued downwards.

The cervical and lumbar enlargements have an evident relation to the large size of the nerves which supply the upper and lower limbs, and which are connected with those regions of the cord. At the commencement of its development in the embryo, the spinal cord is destitute of these enlargements, which, in their first appearance and subsequent progress, correspond with the growth of the limbs.

Fig. 244.

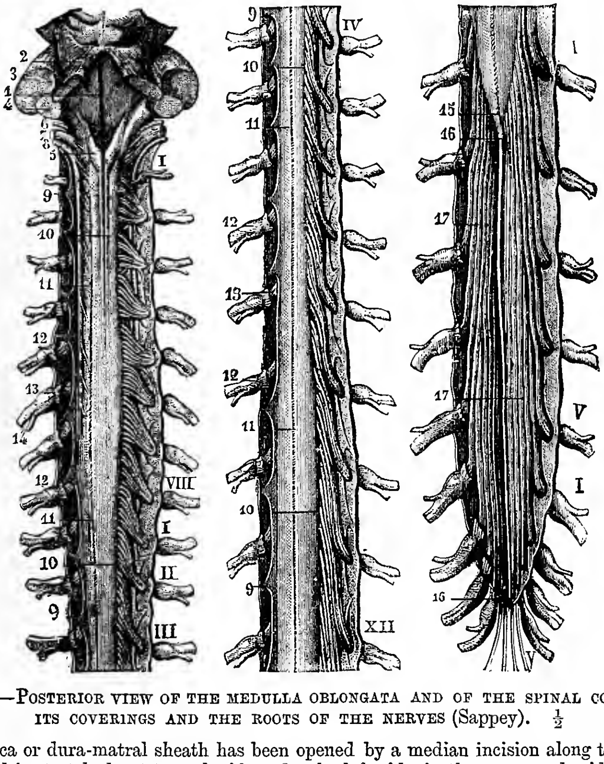


Fig. 244.—Posterior view of the medulla oblongata and of the spinal cord with its coverings and the roots of the nerves (Sappey). $\frac{1}{2}$

The theca or dura-matral sheath has been opened by a median incision along the whole length, and is stretched out to each side. On the left side, in the upper and middle parts (A and B), the posterior roots of the nerves have been removed so as to expose the ligamentum denticulatum, 9, and the anterior roots, 13; and along the right side the posterior roots, 10, are shown arising from the postero-lateral groove, and passing out through the dura mater. The roman numbers indicate the different nerves in the cervical, dorsal, lumbar, and sacral regions respectively; 11, posterior median fissure; 12, ganglia on the posterior roots; 14, the united nerve beyond the ganglion; 15, tapering lower end of the spinal cord; 16, filum terminale; 17, cauda equina.

The **terminal filament** (filum terminale, central ligament) (fig. 245, *b*, *b*) descends in the middle line amongst the nerves composing the cauda equina, and, becoming blended with the lower end of the sheath opposite to the first or second sacral vertebra, perforates the dura mater,

and receiving an investment from it, passes on to be attached with this to the periosteum of the lower end of the sacral canal, or to the back of

Fig. 245.

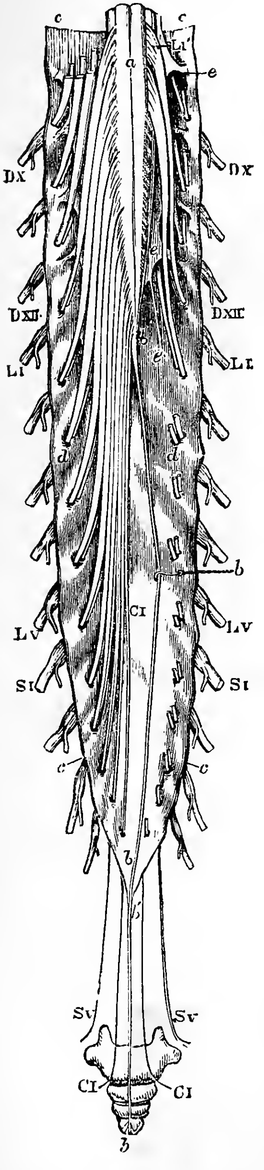


Fig. 245.—POSTERIOR VIEW OF THE LOWER END OF THE SPINAL CORD WITH THE CAUDA EQUINA AND SHEATH (Allen Thomson). $\frac{1}{2}$

The sheath has been opened from behind and stretched towards the sides; on the left side all the roots of the nerves are entire; on the right side both roots of the first and second lumbar nerves are entire, while the rest have been divided close to the place of their passage through the sheath. The bones of the coccyx are sketched in their natural relative position to show the place of the filum terminale and the lowest nerves.

a, placed on the posterior median fissure at the middle of the lumbar enlargement of the cord; *b*, *b*, the terminal filament, drawn slightly aside by a hook at its middle, and descending within the dura-matral sheath; *b′*, *b′*, its prolongation beyond the sheath and upon the back of the coccygeal bones; *c*, the dura-matral sheath; *d*, double foramina in this for the separate passage of the anterior and posterior roots of each of the nerves; *e*, ligamentum denticulatum; Dx, and Dxii, the tenth and twelfth dorsal nerves; Li, and Lv, the first and fifth lumbar nerves; Si, and Sv, the first and fifth sacral nerves; Ci, the coccygeal nerve.

the coccyx. It is a prolongation of the pia mater, enclosing for about half its length an enlarged continuation of the central canal of the cord (see below, p. 268), with a little grey matter near the upper end. Below the termination of the canal, the filum is mainly composed of connective tissue, with blood-vessels prolonged from the anterior spinal vessels, and on either side there run in it three or four small bundles of medullated nerve-fibres, some of which have a few ganglion-cells. These nerve-bundles are regarded by Rauber as representing rudimentary coccygeal nerve-roots. They have no connection with the coccygeal nerves proper.

The filum terminale is distinguished by its silvery hue from the nerves among which it lies.

Fissures.—The spinal cord is incompletely divided into a right and a left half by two fissures which pass in from the middle of the anterior and posterior surfaces, and penetrate through the greater part of its thickness. Of these two *median fissures* the anterior (fig. 246, 1) is wider and therefore more distinct than the posterior, although it does not, in most parts, penetrate to more than one-third the thickness of the cord, while the posterior fissure may reach more than half-way from back to front. The anterior contains a fold of the pia mater and

also many blood-vessels, which are thus conducted to the centre of the cord. At the bottom of this fissure is a transverse connecting portion of white substance named the *anterior* or *white commissure.*

The posterior (fig. 246, 2) is not an actual fissure, for, although the lateral halves of the posterior part of the cord are quite separate, there is no distinct fold of the pia mater between them, but merely a septum of connective tissue and blood-vessels prolonged from that membrane which passes in nearly to the centre of the cord. Its position is marked, especially in the lumbar enlargement and in the cervical region, by a superficial furrow. At its end is the *posterior* or *grey commissure.*

Besides these two median fissures, a lateral furrow is seen on each

Fig. 246.

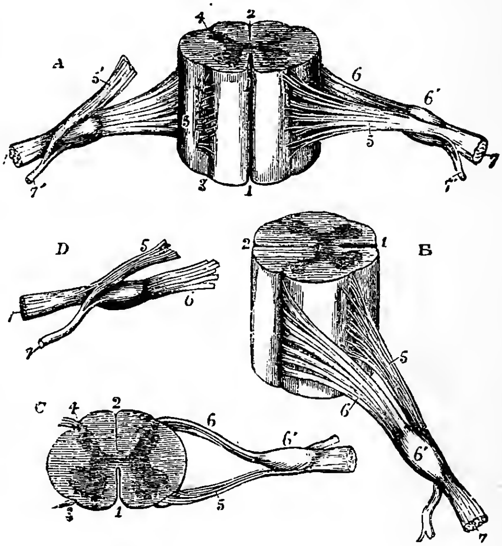


Fig. 246. — Different views of a portion of the spinal cord from the cervical region with the roots of the nerves. Slightly enlarged (Allen Thomson).

In A, the anterior surface of the specimen is shown, the anterior nerve-root of the right side having been divided; in B, a view of the right side is given; in C, the upper surface is shown; in D, the nerve-roots and ganglion are shown from below. 1, the anterior median fissure; 2, posterior median fissure; 3, antero-lateral impression, over which the bundles of the anterior nerve-root are seen to spread (this impression is too distinct in the figure); 4, postero-lateral groove into which the bundles of the posterior root are seen to sink; 5, anterior root; 5′, in A, the anterior root divided and turned upwards; 6, the posterior root, the fibres of which pass into the ganglion, 6′; 7, the united or compound nerve; 7′, the posterior primary branch, seen in A and D to be derived in part from the anterior and in part from the posterior root.

side of the cord, corresponding with the line of attachment of the posterior roots of the spinal nerves. It is named the *postero-lateral groove* (fig. 246, C, 4). Each lateral half of the cord is divided superficially by the postero-lateral groove into a posterior and an antero-lateral part. The attachment of the anterior roots, however, subdivides the latter into anterior and lateral portions.

An antero-lateral groove is often described in the line of origin of the anterior roots of the nerves, but has no real existence. The fibres of these roots in fact, unlike the posterior, do not dip into the spinal cord in one narrow line, but spread over a space of some breadth.

On the posterior surface of the cord, at least in the upper part, there

are two slightly marked longitudinal furrows (fig. 243, 9, 9) situated one on each side, about one millimeter from the posterior median fissure, and marking off, in the cervical region, a slender tract (posterior median column). These are better marked in some individuals than in others.

INTERNAL STRUCTURE OF THE SPINAL CORD: RELATIVE PROPORTIONS OF GREY AND WHITE MATTER.

Grey matter.—When the spinal cord is cut across (figs. 247, 248) it is seen that the grey matter occupies the more central parts, being almost completely enclosed by the white matter. The grey matter appears in the form of two irregularly crescentic portions on either side, united across the middle line by the posterior grey commissure before mentioned, so that its section may be compared in shape to the letter H. The concave side of each lateral crescent faces outwards, and in consequence of the depth of the posterior median fissure the commissure of grey matter joins the crescents nearer their anterior than their posterior ends, except in the lumbar region of the cord.

The two horns or cornua of each crescent are named from their position anterior and posterior: the *anterior cornu* (fig. 247, *a. c*) is the

Fig. 247.

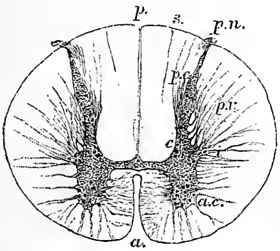


Fig. 247.—Section of the spinal cord in the upper part of the dorsal region (E. A. S.). $\frac{4}{1}$

a, anterior median fissure; *p*, posterior median fissure; *p. n*, posterior nerve-roots entering at the postero-lateral groove; *a. c*, anterior cornu of grey matter; *p. c*, posterior cornu; *i*, intermedio-lateral tract (lateral cornu); *p. r*, processus reticularis; *c*, posterior vesicular column of Clarke; *s*, pia-matral septum forming the lateral boundary of the posterior median column.

shorter and broader, and is everywhere separated from the surface of the cord by white matter which is traversed by the bundles of the anterior roots at the part where these enter the cord. The *posterior cornu* (*p. c*) is longer and narrower, and tapers almost to a point (*apex cornu posterioris*), which closely approaches the external surface of the cord at the postero-lateral sulcus, with which it is connected by fibres of the posterior roots (*p. n*), and between these by processes of the superficial neuroglia. The posterior cornu is slightly narrowed at its base (*cervix cornu*); from that place it gradually expands into the main part of the cornu (*caput cornu*), and from this it tapers in the way just noticed. Near its tip the caput cornu has a peculiar semi-transparent aspect, whence it was named *substantia gelatinosa* by Rolando.

Near the middle of the outer surface of each crescent the grey matter is less sharply marked off than elsewhere from the white matter; portions of grey matter extending into the lateral white column and uniting with one another into what in sections appears like a network enclosing portions of white substance (*p. r*). This is known as the *processus reticularis;* it is best marked in the cervical region (fig. 248, C 5). At

the postero-lateral part of the anterior cornu, immediately in front of the processus reticularis, the grey matter forms in the upper dorsal region (D 1) a somewhat pointed triangular projection, which is sometimes distinguished as the middle cornu but is better known as the *intermedio-lateral tract* (fig. 247, *i*). Above, in the cervical region, this

Fig. 248.

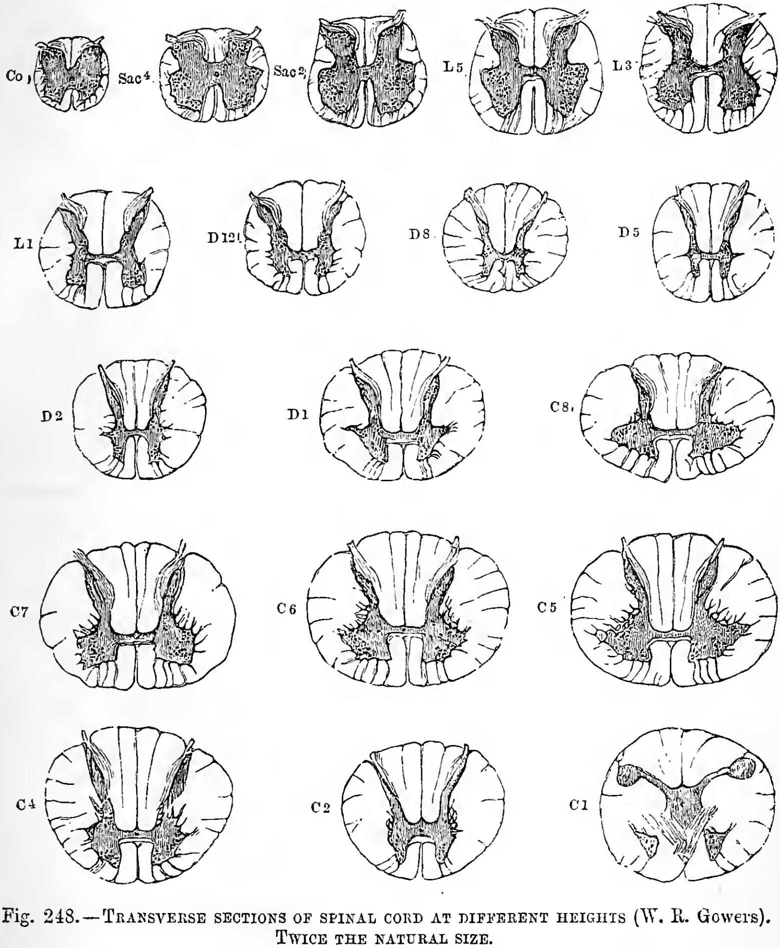


Fig. 248.—Transverse sections of spinal cord at different heights (W. R. Gowers). Twice the natural size.

The letters and numbers indicate the position of each section : Co. at level of coccygeal nerve ; Sac. 4 of 4th sacral ; L3 of 3rd lumbar, and so on. The grey substance is shaded dark, and the nerve-cells within it are indicated by dots.

blends with and forms part of the enlarged anterior cornu ; below, it gradually diminishes and eventually disappears.

The grey crescents vary in form in different parts of the cord (see fig. 248). In the dorsal region both anterior and posterior cornua are narrow. In the cervical and lumbar regions the anterior cornua are

large and broad. The posterior cornua are narrow in the cervical and dorsal, but very broad in the lumbar region. The grey matter is seen in a series of sections to be most abundant in the lumbar region of the cord, and least in the dorsal.

It is clear that what appear in section as irregular crescentic areas of grey matter are in reality long irregularly fluted columns, and that the commissural band uniting the convex edge of the crescents is a flattened expansion, connecting the columns along their whole length. But it is both customary and convenient to speak of the various parts of the grey matter of the cord according to their appearance in sections, although the term "columns" is very generally applied to what appear in section as groups of nerve-cells, occurring in different parts of the grey matter, as well as to the several portions of the white matter immediately to be described.

Fig. 249.

Fig. 249.—Section of lower extremity of spinal cord. Magnified about six times.

The peculiar form of the lower extremity of the central canal is seen.

Central canal.—Extending through the whole length of the spinal cord, in the substance of the grey commissure, there is a minute canal (fig. 247) which, in sections of the cord, is barely visible, as a speck, with the naked eye. It is continued above into the medulla oblongata where it gradually approaches the posterior surface and eventually opens out at the calamus scriptorius of the fourth ventricle. At the lower end of the cord, near the extremity of the conus medullaris, it becomes enlarged, and shaped like the letter T, and is stated by some observers to open on the posterior surface of the cord ; but this is denied by others. This central canal, though minute, is an object of considerable interest as a typical part of the structure of the cord, it being the permanent remains of the ectodermal canal from which the spinal cord is developed. It is more distinctly seen in the lower vertebrata than in mammals.

White matter.—The white substance of each half of the cord completely encloses the grey matter except opposite the posterior cornu. This last therefore serves to separate off a smaller *posterior white column,* which is somewhat wedge-shaped in section and is bounded internally by the posterior median fissure, from the rest of the white substance which forms a large *antero-lateral white column* (figs. 246 to 248). The antero-lateral column is sometimes arbitrarily divided into anterior and lateral white columns, the place of passage of the bundles of the anterior nerve-roots being taken as the limit between the two ; but since these are scattered over a considerable part of the transverse section it is clear that the limit cannot be distinctly fixed.

The white substance is traversed by imperfect septa of connective tissue prolonged inwards from the pia mater. Most of these are irregular and somewhat variable in position, with the exception of one in the cervical region extending inwards towards the grey commissure from the sulcus before described as bounding the posterior median column. This septum (fig. 247, *s*) cuts off a small portion of the posterior column next to the posterior median fissure, corresponding to the projection of the posterior median column on the outside.

The lateral symmetry of the spinal cord is not always perfect. The white columns especially are sometimes found slightly to vary, the varia-

tion being generally caused by the fact that the amount of the pyramidal tracts of white matter differs somewhat on the two sides of the cord (see below, p. 278).

The white matter of the cord, especially that of the lateral column, increases gradually in amount from below upwards, receiving a considerable accession opposite the roots of the larger nerves which supply the limbs. This more sudden increase in the amount of white matter is most marked in the anterior and posterior columns. These relations are strikingly shown in the appended curves (fig. 250) which have been

Fig. 250.

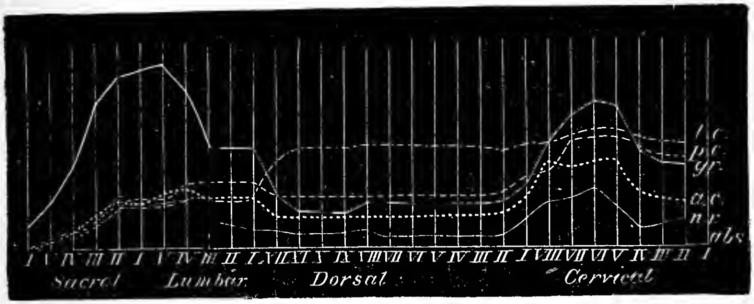


Fig. 250.—Diagram showing both the absolute and relative extent of the grey matter and of the white columns in successive sectional areas of the spinal cord, as well as the sectional areas of the several entering nerve-roots (adapted from Ludwig and Woroschiloff). (E. A. S.)

The sectional areas of the several entering nerve-roots (*n.r*) as well as the extent of the grey matter (*gr*), aud of the lateral, posterior, and anterior columns of white matter (*l. c.*, *p. c.*, and *a. c.*), are represented in superposed curves, the common abscissa of which (*abs.*) is intersected at equal intervals by as many ordinates as there are pairs of spinal nerves. In the ordinates each millimeter above the abscissa represents about one square centimeter of sectional area.

constructed by Ludwig and Woroschiloff from measurements by Stilling. The amount of the grey matter in the different regions is also given, as well as the sectional areas of the roots of the spinal nerves. It is seen that opposite to the origins of the large nerves there is a marked increase in the amount of grey matter.

The anterior or white commissure is likewise proportional in size to the entering nerve-roots.

MICROSCOPIC STRUCTURE OF THE SPINAL CORD.

The white substance of the spinal cord is almost wholly composed of longitudinally coursing medullated nerve-fibres, which in stained transverse sections of the cord (fig. 251) appear as clear rings with a stained dot—the section of the axis-cylinder—either in the middle of the ring or shifted somewhat to one side. The fibres vary much in size, and in many parts of the section larger and smaller fibres are intermixed, but some parts are characterized by containing many large fibres, others for the most part small fibres. The largest fibres are in the posterior part of the lateral column, the smallest in the part of the lateral column in the neighbourhood of the processus reticularis, but the fibres of the

posterior median column are also very small. The white columns are imperfectly divided into secondary columns by incomplete septa of fibrillar connective tissue which are prolonged inwards from the inner layer of the pia mater, and convey bloodvessels to the interior of the cord.

Fig. 251.

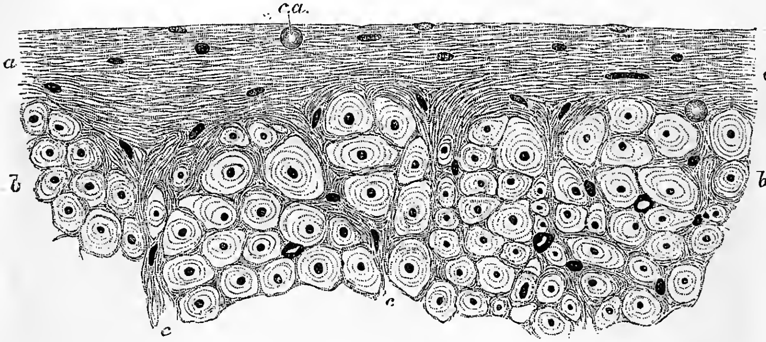


Fig. 251.—A small portion of a transverse section of the human spinal cord. Highly magnified. (E. A. S.)

a, *a*, superficial neuroglia; *b*, *b*, transverse section of part of the lateral column of the cord in which the dark points are the axis-cylinders, and the clear areas the medullary substance of the nerve-fibres: the superficial neuroglia is seen to exhibit the appearance of a fine network in which numerous nuclei and one or two *corpora amylacea* (*c. a*) are embedded, and to extend inwards among the nerve-fibres.

Immediately beneath the pia mater and closely investing the cord externally is a layer of what in the fresh condition appears a homogeneous or finely granular substance with nuclei embedded in it here and there. In sections of the cord hardened in alcohol or chromic acid, the substance in question is finely reticulated (fig. 251, *a*, *a*). The layer which it forms is very thin over some parts of the surface but comparatively thick in others, and where the pia-matral septa pass into the cord, it accompanies and invests them and their ramifications in the white substance, passing with them between the irregular bundles of nerve-fibres. Not only does this subpial reticular substance accompany the prolongations of the fibrillar tissue and largely assist in forming the incomplete septa above mentioned, but it extends independently amongst the individual nerve-fibres, occupying the interstices between them, and serving as a uniting medium in which they are embedded. Hence it was named by Virchow the *neuroglia*. The nuclei in it belong for the most part to small cells (neuroglia-cells) which occur in considerable numbers in some parts of the tissue; but others to more conspicuous cells, known as the cells of Deiters, which are stellate in section and are found here and there in the larger interstices between the nerve-fibres. Along the line of origin of the posterior roots the superficial neuroglia is prolonged into the cornu of grey matter, and expands in it to form the substantia gelatinosa of Rolando. This, as before mentioned, presents a transparent jelly-like appearance in the fresh condition, but in sections of the hardened cord it is finely reticular,

containing numerous neuroglia-cells, and a few bloodvessels. Some of the bundles of nerve-fibres of the posterior root traverse this substance, and it contains, especially near the cornu proper and the posterior white column, a few small scattered nerve-cells; but on the whole there are fewer true nervous elements in it than in any other part of the cord.

In the constitution of the rest of the cornua the neuroglia takes part to a far less extent than in the substantia gelatinosa. It is true that it is prolonged both from this and from the white substance into the grey matter, and pervades the latter throughout in every part. But it is largely obscured in this situation by the proper nervous elements, which in the grey substance are of three kinds. In the first place are found multipolar nerve-cells, mostly of large size, scattered singly or occurring in groups throughout the grey substance. Secondly, in connection with these and especially accumulated around the cells and cell-groups, is an interlacement of the finest nerve-fibrils, which is derived according to Gerlach from the ramification of the nerve-cells, and may be the medium of communication between the several cells of a group or even between separate cells and groups. Thirdly, occupying a considerable portion of the grey matter, are nerve-fibres, mostly of the medullated kind, and the axis-cylinder processes of the nerve-cells; these traverse the grey matter in different directions, coursing for the most part in bundles which intercross with one another, and confer on the grey matter a spongy appearance. Hence it is sometimes known as the *substantia spongiosa.*

The neuroglia is generally assumed to be a modified form of connective tissue. Kühne and Ewald find, however, that the tissue composing the substantia gelatinosa of Rolando (and probably the neuroglia-tissue generally) is similar in chemical nature to the network described by them in the medullated sheath of the nerves, and named "neuro-keratin" from its apparent nature and the resistance which it offers to the action of digestive fluids (see p. 144). But this resisting power appears to be conferred upon the tissue by the action of alcohol, for in the fresh state it is quite soft, and easily dissolved by the fluids in question. So that the argument in favour of its ectodermal origin which is sometimes drawn from the supposed chemical constitution of the substance, is not sufficiently strong to negative the view, originally taught by Kölliker, that the neuroglia (or *reticulum* as he termed it) is a peculiar form of connective tissue (allied to retiform tissue) derived, together with the connective tissue septa which it accompanies, by ingrowth from the mesoderm surrounding the embryonic central nervous system. The presence of the neuroglia-cells in it, which resemble in general appearance small connective tissue cells, is in favour of Kölliker's view.

Small concentrically striated globules, termed *corpora amylacea,* are very frequently met with in the neuroglia of the cord, as well as in many of the parts of the central nervous axis. They appear to be composed of proteid substance but, although long recognized, their mode of formation and their meaning are still entirely unknown.

Arrangement of the nerve-cells in the grey matter. In transverse sections of the cord it is seen that the nerve-cells are not by any means equally distributed throughout the grey substance, but are arranged in definite groups, which occupy the same relative position in successive sections. The groups are therefore the sections of longitudinal tracts of grey matter rich in nerve-cells, and named the *ganglionic,* or *vesicular columns* of the grey matter. The longitudinal continuity of the groups can be seen in sections of the cord made parallel with its long axis and passing through the part of the grey matter where the groups occur.

Of these groups or columnar tracts of nerve-cells, the one which is most constant and contains the largest cells is found along the whole of the anterior part of the anterior cornu where the nerve-cells lie among the entering fibres of the anterior roots. There seems to be little doubt that many of these anterior or motor nerve-fibres are directly continuous with the axis-cylinder processes of some of the nerve-cells of this group.

Fig. 252.

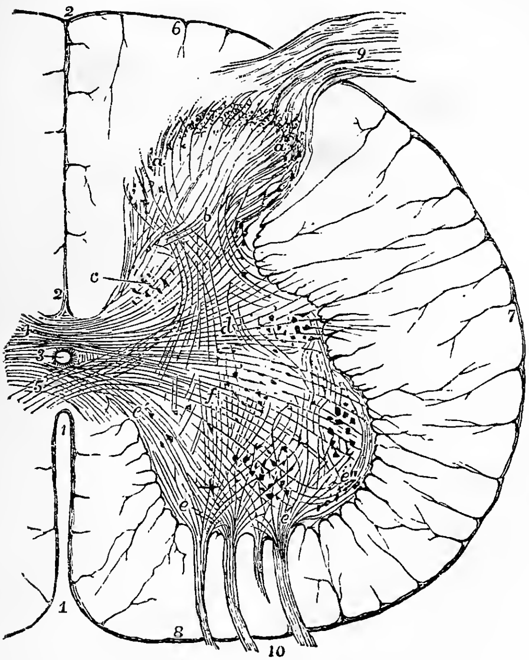


Fig. 252. — Transverse section of half the spinal marrow in the lumbar enlargement (Allen Thomson). $\frac{8}{1}$

This is a semidiagrammatic representation taken from a specimen, and founded in part on the statements of Lockhart Clarke and of Kölliker.

1, anterior median fissure; 2, posterior median fissure; 3, central canal lined with epithelium; 4, posterior commissure; 5, anterior commissure; 6, posterior column; 7, lateral column; 8, anterior column; 9, fasciculus of posterior nerve-root entering in one bundle, a part of which passes into the posterior cornu, and a part into the posterior column; 10, fasciculi of anterior roots; *a*, *a*, caput cornu posterioris with the gelatinous substance of Rolando; *b*, the cervix cornu; *c*, posterior vesicular column of Clarke; to the right of *d*, the group of cells in the intermedio-lateral tract; *e*, *e*, fibres of the anterior roots, entering the anterior cornu, and passing through among the cells; *e′*, fibres from the anterior roots which decussate in the anterior commissure; *e″*, external fibres from the roots running round the outside of the anterior grey cornu towards the lateral columns; *f*, fibres from the posterior commissure and from the posterior cornu running towards the anterior. Three groups of cells are seen in the anterior cornu in this region of the cord; and from their position may be described as external, internal, and posterior.

Hence it is sometimes named the *motor ganglionic column*, but it is more generally known as the *ganglionic or vesicular column of the anterior cornu.* Its cells are in some parts collected into two groups, a lateral nearer the lateral column of white matter, and a mesial nearer the anterior column; in the lumbar enlargement there is a third, more deeply seated, posterior group (fig. 252). Some of the cells which are nearer the anterior commissure send their axis-cylinder processes through this to the other half of the cord: it is believed that these processes may be connected with nerve-fibres of the corresponding anterior root of the other side.

In some of the lower vertebrates it may be made out that there are variations in the size of this column of cells in successive portions of the cord, the cells being more numerous opposite the points of entrance of the nerve-roots, the attachment of which to the cord is in them more localized than in man and higher vertebrates. In this way somewhat of a segmental formation of the column is indicated, and in some fishes and reptiles the enlargement of the group of cells and its enclosing grey matter is sufficiently marked to produce an external swelling opposite each nerve-pair.

Fig. 253.

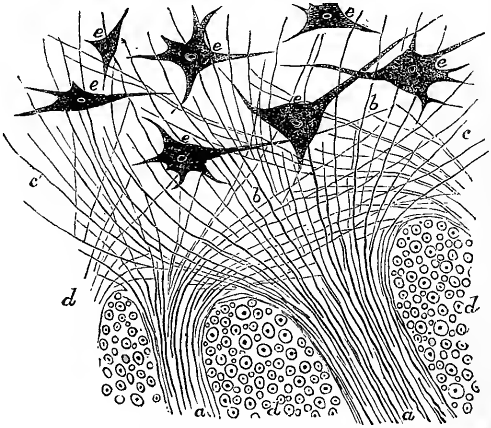


Fig. 253.—A SMALL PORTION OF A TRANSVERSE SECTION OF THE SPINAL CORD AT THE PLACE WHERE TWO BUNDLES OF THE FIBRES OF THE ANTERIOR ROOTS PASS INTO THE GREY SUBSTANCE. (Allen Thomson.) $\frac{1}{300}$

a, a, two bundles of fibres of the anterior root passing through the white substance of the cord, *d, d*; *b, b,* fibres running backwards through the grey substance towards the posterior cornua; *c, c′*, others spreading in the anterior cornua, on the one side towards the anterior commissure, and on the other round the outer side of the anterior cornu; *e, e,* large multipolar cells in the grey substance of the anterior cornu; the communication between these cells and some of the nerve-fibres of the roots is not shown in the figure.

A second very well marked group or column of cells, which occupies in transverse section an area at the inner or mesial angle of the base of the posterior cornu (fig. 252, *c*), and appears cut off from the rest of the grey matter by a curved bundle of fibres derived from the posterior root, extends along the middle region of the cord from the third lumbar to the seventh cervical nerve. This was termed by Lockhart Clarke the *posterior vesicular column*; it is often known as *Clarke's column.* It is largest in the lower part of the dorsal region. From the fact that it is almost entirely confined to that region of the cord it was termed by Stilling the dorsal nucleus. But although ceasing above and below the points mentioned, it is not altogether unrepresented in other parts, for groups of cells are found in a similar situation opposite the origin of the second and third sacral nerves (sacral nucleus of Stilling) and opposite the origin of the third and fourth cervical nerves (cervical nucleus); and elsewhere there are scattered cells in the same part of the section of the cord. The cells of this column are of moderate size, and their axis-cylinder processes tend for the most part towards the lateral column. It is noteworthy that Clarke's column is best developed in the region of the cord where the column of the anterior cornu is least so.

A third column of cells lies in the intermedio-lateral tract (*column of the intermediolateral tract,* fig. 252, *d*). Like that tract, the ganglionic column it contains only appears as a distinct formation in the dorsal region; in other parts it blends more or less with the column of the

anterior cornu. Its cells, although large, are on the whole smaller than those of the anterior cornu. In the upper part of the cervical region a group of cells becomes distinct in a similar situation, and is traversed by the roots of the spinal accessory nerve.

The above are the chief groups or columns of cells which are distinguishable in transverse section, and of them the column of the anterior cornu is the only one which can be described as extending along the whole length of the cord. But in addition to the groups, a certain number of scattered cells are met with, distributed through the posterior

Fig. 254.

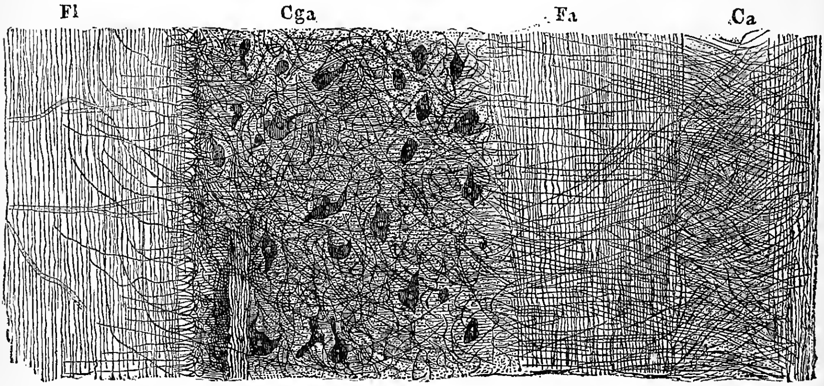


Fig. 254.—Longitudinal section of the cord through the anterior white commissure and anterior grey cornu. Dorsal region. (Henle). $\frac{40}{1}$

Only the left half of the section is represented.

Ca, anterior commissure with fibres passing into it through the anterior column from the grey matter, and decussating with those of the other side; *Fa*, anterio white column; *Cga*, anterior cornu of the grey matter; many of the multipolar cells are extended in a longitudinal direction; *Fl*, lateral column, into which fibres are seen passing from the grey cornu and turning upwards in a longitudinal direction.

cornu, and extending into the substantia gelatinosa of Rolando. These cells vary much in form and size, but are for the most part spindle-shaped and smaller than those previously mentioned. It is not known whether they have any special relation to the fibres of the posterior roots, although in the lamprey it has been shown by Freud that cells which appear to correspond with them send their axis-cylinders into those roots.

Commissures.—The *anterior commissure* (fig. 254, *Ca*) consists of medullated nerve-fibres which pass on each side, some into the anterior white column, others into the anterior horn of grey matter. Their course is not strictly transverse, many fibres which enter the anterior part of the commissure at one side leave it at the posterior portion on the other side. There is thus a double decussation at the middle line (fig. 252, 5). This decussation is most distinctly seen in the comparatively short and wide commissure of the lumbar region, and in the upper part of the cervical region. In the latter situation it appears as a continuation of the decussation of the anterior pyramids of the medulla oblongata, to be afterwards described. In addition to the transverse there are a few longitudinal bundles of fibres. The transverse fibres of the anterior commissure

are often somewhat displaced by vessels which pass into the grey substance from the anterior fissure.

The *posterior commissure* is also composed of medullated fibres running transversely or with a slight obliquity, but there is a considerable amount of neuroglia between them, and this gives the grey aspect to the commissure. In this commissure is contained the central canal of the spinal cord, the fibres of the commissure sweeping round it, leaving an area outside the epithelium of the canal almost free from nerve-fibres, and occupied only by what appears like a portion of neuroglia, having in the hardened condition a reticulated structure and in the fresh state a gelatinous aspect. It is sometimes termed *substantia gelatinosa centralis*. The outermost part is marked off from the rest by the more concentric disposition of its fibrils. There is rather more of the posterior commissure behind the central canal than in front. The fibres of the posterior part curve backwards on reaching the lateral crescents of grey matter and pass towards the bundles of the posterior roots, whereas those of the anterior part diverge at various angles into the cervix cornu.

The *central canal* is lined with a layer of columnar ciliated epithelium. The cells are slightly longer on the dorsal than on the ventral aspect of the canal. Each cell is provided with a bunch of cilia on the side which is turned towards the lumen of the canal: the other end of the cell is prolonged into the reticular substance just mentioned, and there becomes lost to view.

In the adult the lumen of the central canal is not unfrequently obliterated, being filled up by detached cells.

Origin of the spinal nerves.—The anterior and posterior roots of the spinal nerves are attached along the sides of the cord, opposite to the corresponding cornua of the grey matter; the posterior roots in a straight line at the postero-lateral groove, and the anterior roots scattered somewhat irregularly upon the surface (fig. 246, B).

The anterior roots are seen in a transverse section to pass through white substance and to enter the grey cornu in several bundles, which have a slight upward inclination, so as to be often cut obliquely if the section be exactly in a transverse plane. Some of the fibres on reaching the grey matter are directly connected with the axis-cylinder processes of the large nerve-cells of the cornu. The others, and perhaps the larger number, pass by the cells without, so far as can be seen, entering into relation with them.

As soon as the bundles enter the grey matter, their fibres diverge from one another, some going inwards towards the anterior commissure, others outwards towards the anterior part of the lateral column and others straight backwards to the posterior cornu (fig. 255). Of those which pass inwards some are continued into the axis-cylinder processes of the mesial group of cells of the anterior cornu, and others are stated to go to the other side of the cord through the anterior commissure and perhaps to become connected with the corresponding cells there. The outwardly directed fibres of the root are partly connected with the lateral group of anterior cornu cells, and partly enter the lateral white column and turn upwards in it. The middle set of fibres again are partly connected to the cells of the lateral group of the anterior cornu, and partly, as just mentioned, pass on to the posterior cornu without coming into relation with the motor nerve-cells. Their further course here has not been traced. According to Gerlach they are continued into some of the scattered cells of the posterior cornu.

The posterior roots at their entrance into the cord are seen to form two sets. Of these the external and somewhat smaller enters the grey matter at once, passing in separate bundles, partly through the substantia gelatinosa of Rolando, partly curving round this substance. Their course, like that of the bundles of the anterior roots, is directed slightly obliquely upwards. In the substantia gelatinosa many of the bundles become longitudinal, turning either upwards or

Fig. 255.

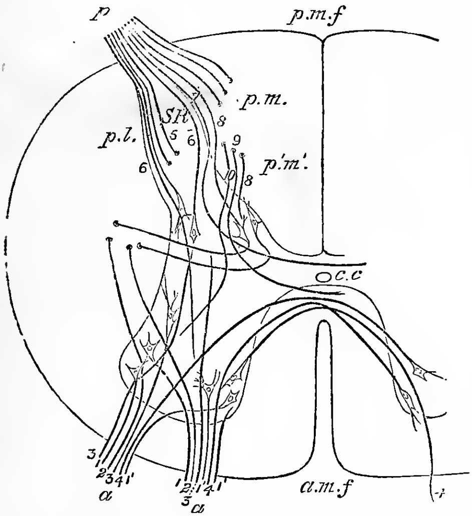


Fig. 255.—Diagram to illustrate the course taken by the fibres of the nerve-roots on entering the spinal cord. (E.A.S.)

a, *a*, two funiculi of the anterior root of a nerve; 1, 1, some of their fibres passing into the lateral cells of the anterior cornu; 1′, 1′, others passing into the mesial cells of the same cornu; 2, 2, fibres passing to the lateral column of the same side without joining nerve-cells; 3, 3, fibres passing towards the posterior cornu; 4, 4, fibres passing across the anterior commissure, to enter nerve-cells in the anterior cornu of the other side; *p*, funiculus of the posterior root; *p*, *l*, fibres of its lateral or external division coming through and around the gelatinous substance of Rolando; some of these, 5, are represented as becoming longitudinal in the latter; others, 6, 6, as passing towards the anterior cornu, either directly or after joining cells in the posterior cornu, and others, 7, as curving inwards towards the grey commissure; *p*, *m*, fibres of the mesial or inner division, entering the posterior column and then becoming longitudinal; *p′*, *m′*, fibres from a posterior root which had joined the cord lower down and entered the posterior column, now passing into the grey matter at the root of the posterior cornu. Of these, 8, is represented as entering Clarke's column, 9, as curving around this and coursing to the anterior commissure, and 10, as passing towards the anterior cornu. The axis-cylinder processes of the cells of Clarke's column are shown arching round, and taking the direction of the lateral column.

a.m.f., anterior median fissure; *p.m.f.*, posterior median fissure; *c.c.*, central canal; *s.R.*, substantia gelatinosa of Rolando.

downwards for a certain distance, and then in all probability passing in again horizontally. The rest pass at once horizontally into the grey matter where for the most part they become lost, but some can be traced as far as the anterior cornu, and others tend towards the posterior commissure, and probably pass through it to the other side.

The inner or principal bundle of the posterior root enters the posterior white column. The fibres turn upwards in this and run longitudinally for some distance. At length, after passing through several segments of the cord, they turn in obliquely into the base of the posterior cornu, which in their longitudinal course they have been gradually approaching. (It is uncertain whether all the fibres thus turn in again or whether some are continued along the column towards the encephalon.) Here they form a well-marked bundle, which traverses the grey matter obliquely,

passing towards the anterior cornu, and cutting off in their passage a distinct area of the grey substance in which, in the dorsal region, the cells of Clarke's column lie. Some of the fibres of the bundle enter this area and there become longitudinal, others go towards the outer or lateral group of cells of the anterior cornu, and others again bend sharply round towards the anterior commissure.

Course of the nerve-fibres in the spinal cord.—It is impossible to unravel the tracts of nerve-fibres in their passage along the spinal cord, and it is exceedingly difficult to trace the same fibre or fibres for any distance in microscopical sections of the organ. But the task of following out the course of certain sets of fibres has been much facilitated of late years by the application to the subject of certain special developmental and pathological methods of observation. Thus it is found that if the development of the spinal cord is carefully observed, the medullary substance of the nerve-fibres is formed later along certain tracts of the white columns than in the rest of the white matter, so that in transverse sections of the cord these tracts are easily distinguishable by their more transparent grey appearance (Flechsig).

Another method by which similar results are arrived at consists in tracing the course which the degeneration of the fibres pursues in consequence of a lesion either in the encephalon, or in the spinal cord itself, or even in the peripheral nerves; the lesions being produced by accidental injury, by pathological changes, or experimentally in animals (Schiefferdecker). The degenerations which follow are either the result of the Wallerian law that separation of a nerve-fibre from the nerve-cell with which it is connected as its trophic (nutritive) centre is followed by degenerative changes in the part of the fibre thus separated from that centre, or they may follow from the prolonged disuse of a nervous tract, especially in young animals, as when a limb is removed altogether or a nerve or nerves permanently paralyzed. The degeneration which follows a lesion of part of the nervous centre, and especially section of the spinal cord, is in some tracts centrifugal, in others centripetal. The place of the degenerated nervous substance is taken by connective tissue and this, by its difference of behaviour to staining fluids, can easily be distinguished by the surrounding undegenerated white substance. In some cases groups of nerve-cells are affected by the degenerative processes, and some of the cells may even eventually disappear altogether. When this is the case it may be assumed that they are in some way in connection with the tracts of fibres which have simultaneously undergone degeneration.

In the **antero-lateral column** there are at least two such tracts which can by these methods be traced not only along the greater part of the spinal cord but into or from certain parts of the encephalon. The two tracts in question have accordingly been named, from their upper connexions, the *pyramidal tract* or *tracts*, and the *direct lateral cerebellar tract*.

The *pyramidal tract* is directly traceable down from the anterior pyramid of the medulla oblongata. The greater number of the fibres which compose the pyramid, cross at the upper limit of the spinal cord, down which they pass in the posterior part of the lateral column as a compact bundle of fibres occupying in transverse section a somewhat oval area which lies in the angle between the posterior cornu and the outer surface of the cord, but is in most parts separated from both by bundles of fibres belonging to other systems. This *lateral* or *crossed part of the pyramidal tract* (fig. 256, *c.p.t.*) can be traced as far as the third or fourth pair of

sacral nerves, becoming gradually smaller below and approaching the surface of the cord.

Some of the fibres of the pyramids of the medulla do not decussate at the upper limit of the cord. These pass down close to the anterior median fissure, forming the *anterior* or *uncrossed portion of the pyramidal tract* (*d.p.t.*), which gradually diminishes as it is traced downwards, and ceases altogether at about the middle or end of the dorsal region of the cord. It is highly probable that the decussation of these anterior pyramidal tracts goes on along their whole course, their fibres passing

Fig. 256.

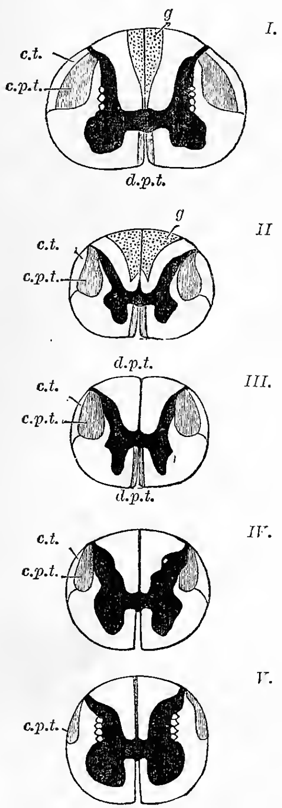


Fig. 256.—Diagrammatic sections of the spinal cord at different parts to show the chief localized tracts of fibres in the white substance (after Flechsig). One and a half times the natural size.

I., at the level of the sixth cervical nerve; *II.*, of the third dorsal; *III.*, of the sixth dorsal; *IV.*, of the twelfth dorsal; *V.*, at the level of the fourth lumbar.

d.p.t., direct or anterior pyramidal tracts; *c.p.t.*, crossed or lateral pyramidal tracts; *c.t.*, direct cerebellar tract; *g*, tract of Goll.

through the anterior commissure and through the grey matter of the opposite side to reach the lateral pyramidal tract on the other side of the cord. The decussating fibres in the anterior commissure would thus form a continuation of the larger decussation in the medulla oblongata.

There is much variation in the development of the anterior pyramidal tracts in different individuals. In some they are so well marked as to form a visible prominence on the surface of the cord close to the anterior median fissure, in others they are quite small, or may even fail altogether. In this case it may be assumed that the decussation of the pyramids, which is known to be subject to considerable variation, has been more complete than usual. In other cases again the anterior pyramidal tracts may be unsymmetrical, being more developed on one side than on the other, or the tract on one side may be wholly undeveloped.

The *direct lateral cerebellar tract* (*c.t.*) lies between the lateral pyramidal tract and the outer surface of the cord, occupying a somewhat narrow area of the transverse section, which in the upper regions of the cord reaches to the tip of the posterior cornu, but lower down becomes more limited, and is separated from the cornu by the intervention of the adjoining pyramidal tract. It disappears at about the second or third lumbar nerves.

It is found that there are a few fibres scattered through the neighbouring parts of the lateral column which, from their development

simultaneously with those of the cerebellar tract, should be apparently reckoned with it. In the same way a few fibres of the pyramidal tract are found scattered in other parts of the antero-lateral column. It is stated that the axis-cylinder processes of some of the cells of Clarke's column are in connexion with the fibres of this lateral cerebellar tract.

The fibres of this tract acquire their medullary sheath somewhat later than those of the pyramidal tract, and are hence distinguishable from them.

The remainder of the antero-lateral column has so far not been mapped out in definite tracts. It varies in sectional area with the size of the nerve-roots and of the grey matter. This is especially the case with the anterior part, that is to say, the anterior column minus the anterior pyramidal tract, which is distinguished by Flechsig as the *principal tract of the anterior column*, and its fibres not improbably are of a commissural nature, serving to connect the grey matter of different segments of the cord. It receives fibres from the grey matter of the other side through the anterior commissure (fig. 254), perhaps directly prolonged from the anterior root of the other side, and also small bundles from the anterior cornu of the same side.

In the **posterior white column** there is a tract which can be traced in the same way as those in the antero-lateral column, but extends only as far as the middle of the dorsal region of the cord. This tract corresponds with the situation of the posterior median column, and is known as *Goll's tract* (fig. 256, *g*). Its fibres are continued, according to Flechsig, from the axis-cylinders of some of the cells of Clarke's column, partly from the same side of the cord, partly through the posterior commissure from the other side.

The rest of the posterior column in the upper regions of the cord and the whole of it in the lower appears chiefly to be formed by the inner bundles of the fibres of the posterior roots, which pass upwards in it before turning in to the grey substance. It increases gradually in sectional area from below upwards, with a more sudden increase opposite the lumbar and cervical enlargements.

There was formerly much discussion as to the ultimate destination of the fibres of the nerve-roots in the cord, some holding with Volkmann that none of them reached the brain, arguing from measurements of the size of the cord in different regions, that the cord could not contain in its upper regions all those nerve-fibres which were traceable to it in the lower; others with Kölliker taking the view that the diminished size of the nerve-fibres in the upper regions, might fully account for the insufficient enlargement in sectional area, without supposing that any of the fibres became lost in the grey matter. But apart from the fact that an actual connexion of the fibres of the nerve-roots with nerve-cell prolongations has now been shown in a number of instances, Stilling has proved by actual observation and calculation that there are not quite half as many fibres in a transverse section of the white substance in the upper cervical region as reach the cord by the nerve-roots. Thus in one subject it was found that about 800,000 fibres entered the cord by the roots (500,000 by the posterior roots, and 300,000 by the anterior), while the white substance at the level of the second cervical nerve contained only about 400,000 fibres.

THE ENCEPHALON.

The encephalon comprises the medulla oblongata, the cerebellum with the pons Varolii, the mesencephalon, the thalamencephalon, and the cerebral hemispheres; the three parts last named being termed collectively the cerebrum. The *medulla oblongata* (fig. 257, D) is the part continuous with the spinal cord: it is the lowest part of the encephalon and rests against the basilar process of the occipital bone. The *cerebellum* (B) occupies the posterior fossa of the cranium. Its central part forms the posterior boundary of a space, which is bounded in front by the posterior surface of the medulla oblongata, and which is named the fourth ventricle of the brain. On each side of this, the cerebellum is connected by peduncles below with the medulla oblongata, above with the cerebrum, and in the middle with the *pons Varolii* (C), a commissure uniting the two halves of the cerebellum. The *cerebrum* (A) includes all the remaining and by far the largest part of the encephalon. It is united with the parts below by a comparatively narrow and constricted portion or *isthmus* (*a*, *b*), part of which, forming the crura cerebri, descends through the pons Varolii into the medulla oblongata, whilst another part on each side joins the cerebellum. The cerebrum is mainly composed of the large convoluted cerebral hemispheres, and within it are the third and two lateral ventricles. It occupies the vault of the cranium, the anterior and middle cranial fossæ, and the superior fossæ of the occipital bone. The cerebral hemispheres are united together by a large commissure termed the corpus callosum, and by smaller commissures.

Fig. 257.

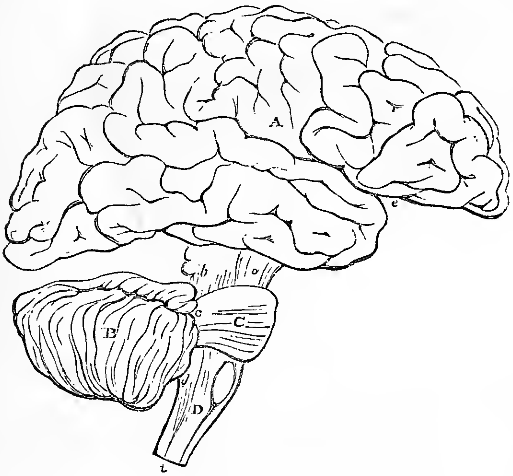


Fig. 257.—Plan in outline of the encephalon, as seen from the right side. $\frac{1}{3}$

The parts are represented as separated from one another somewhat more than natural so as to show their connections. A, cerebrum; *e*, fissure of Sylvius; B, cerebellum; C, pons Varolii; D, medulla oblongata; *a*, peduncles of the cerebrum; *b*, *c*, *d*, superior, middle, and inferior peduncles of the cerebellum; the parts marked *a*, *b*, form the isthmus encephali.

THE MEDULLA OBLONGATA.

EXTERNAL CHARACTERS.

The *medulla oblongata* is continuous below with the spinal cord, on a level with the lower margin of the foramen magnum. Its upper limit is

marked by the lower border of the pons Varolii, into which it is continued above; its anterior or ventral surface rests in the basilar groove, whilst posteriorly it is received into the fossa named the vallecula between

Fig. 258.

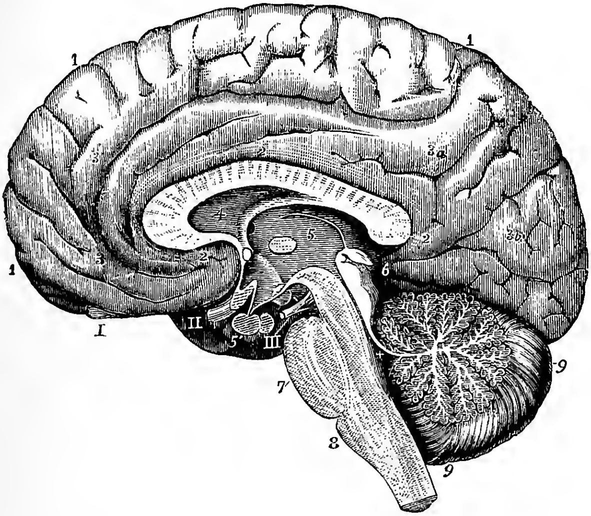


Fig. 258.—Right half of the brain divided by a vertical antero-posterior section (from various sources and from nature). (Allen Thomson). ½

1, 2, 3, 3*a*, 3*b*, are placed on convolutions of the cerebrum; 4, the fifth ventricle, and above it the divided corpus callosum; 5, the third ventricle; 5′, pituitary body; 6, corpora quadrigemina and pineal gland; +, the fourth ventricle; 7, pons Varolii; 8, medulla oblongata; 9, cerebellum; I, the olfactory bulb; II, the right optic nerve; III, right third nerve.

the hemispheres of the cerebellum, and there bounds the fourth ventricle. From its sides the seventh to the twelfth cranial nerves issue.

The term medulla oblongata, as employed by Willis and Vieussens, and by those who directly followed them, included the crura cerebri and pons Varolii, as well as that part to which by Haller first, and by most subsequent writers, this term has been restricted.

It has the form of an irregular truncated cone, being expanded at its upper part both laterally and dorso-ventrally: its length from the lower part of the decussation of the pyramids to the pons is nearly an inch (20 to 24 mm.); its greatest breadth is about three fourths of an inch (17 to 18 mm.); and its thickness, from before backwards, rather less (15 mm.). In its lower part where it joins the spinal cord, its measurements are but little different from those of the cord.

The *anterior* and *posterior median fissures* which partially divide the spinal cord are continued up into the medulla oblongata. The anterior fissure terminates immediately below the pons in a recess, the *foramen cæcum* of Vicq d' Azyr; it is partly interrupted below by the decussating

bundles of the pyramids; the posterior fissure is continued upwards to about the middle of the medulla where it expands into the fourth ventricle.

The structure of the medulla oblongata will be most easily made clear by tracing the several parts of the spinal cord upwards in their continuity with the parts of the medulla oblongata.

Fig. 259.

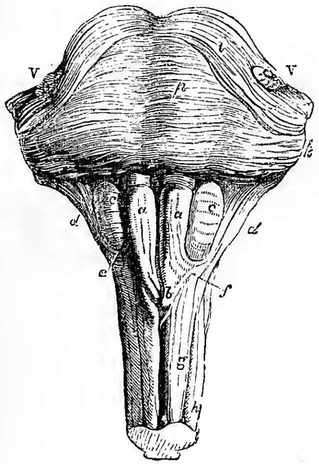


Fig. 259.—View of the anterior surface of the pons Varolii and medulla oblongata, with a small part of the spinal cord attached.

a, a, pyramids; *b,* their decussation; *c, c,* olives; *d, d,* restiform bodies; *e,* external arciform fibres, curving round the lower end of the olive; *f,* fibres described by Solly as passing from the anterior column of the cord to the cerebellum; *g,* anterior column of the spinal cord; *h,* lateral column; *p,* pons Varolii; *i,* its upper fibres; v, v, roots of the fifth pair of nerves.

In doing this it will be found that the relative position and extent of many of the parts are gradually altered, and that other parts which are not, so far as is known, represented in the spinal cord become interpolated between those which are there met with. It will further be found that the change of relative position of the parts is largely owing to two causes. In the first place the sudden passage of large bundles of medullated fibres from the posterior part of the lateral column of the cord to the opposite side of the anterior median fissure appears to break up to a great extent the grey matter of the anterior cornu, which is traversed by the bundles. In the second place the opening up of the central canal and separation of the lips of the posterior median fissure bring the grey matter to the surface in the fourth ventricle, whilst the posterior cornu is coincidently shifted to the side, much in the same way as it would be if a median incision were made from the posterior surface of the spinal cord into the central canal, and the two lateral halves were then turned outwards so that the sides of the posterior median fissure became the posterior surface of the cord.

In tracing the parts of the spinal cord upwards into the medulla in the manner proposed, we may employ the lines along which the cranial nerve-roots issue from the sides of the medulla as guides in recognizing in the latter the three chief columns which are marked off on the surface of the cord by the exit of the spinal nerve-roots. It will be found that the *line of the posterior or sensory roots* of the spinal nerves is prolonged for a certain distance by a series of bundles of the spinal accessory or eleventh cranial nerve(figs. 260, 261, *XI*). This begins to take origin as far down as the lower end of the cervical region of the cord (fig. 244, 8), but there its roots issue more from the side, and external to the posterior roots of the cervical nerves. At the upper end of the cervical region however, they approach the line of the posterior roots, and indeed some of the bundles arise in conjunction with those of the first and sometimes of the second cervical nerve, after which, as just

mentioned, they prolong the line of the posterior roots. They are succeeded along this line by the bundles of the vagus root (fig. 260, *X*), and these again by those of the glossopharyngeal (*IX*). On tracing

Fig. 260.

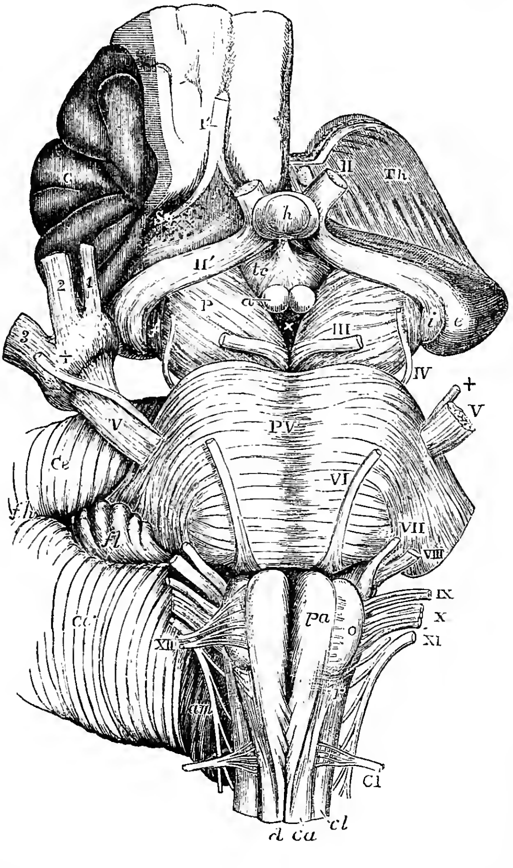


Fig. 260.—View from before of the medulla oblongata, pons Varolii, crura cerebri, and other central portions of the encephalon. (Allen Thomson) Natural size.

On the right side the convolutions of the central lobe or island of Reil have been left, together with a small part of the anterior cerebral convolutions: on the left side these have been removed by an incision carried between the thalamus opticus and the cerebral hemisphere.

1′, the olfactory tract cut short and lying in its groove; II, the left optic nerve in front of the commissure; II′, the right optic tract; *Th*, the cut surface of the left thalamus opticus; C, the central lobe or island of Reil; *Sy*, fissure of Sylvius; × ×, anterior perforated space; *e*, the external, and *i*, the internal corpus geniculatum; *h*, the hypophysis cerebri or pituitary body; *tc*, tuber cinereum with the infundibulum; *a*, one of the corpora albicantia; P, the cerebral peduncle or crus; *f*, the fillet; III, close to the left oculo-motor nerve; ×, the posterior perforated space.

The following letters and numbers refer to parts in connection with the medulla oblongata and pons. PV, pons Varolii; *V*, the greater root of the fifth nerve; +, the lesser or motor root; *VI*, the sixth nerve; *VII*, the facial; *VIII*, the auditory nerve; *IX*, the glossopharyngeal; *X*, the pneumogastric nerve; *XI*, the spinal accessory nerve; *XII*, the hypoglossal nerve; C I, the suboccipital or first cervical nerve; *p a*, pyramid; *o*, olive; *d*, anterior median fissure of the spinal cord, above which the decussation of the pyramids is represented; *c a*, anterior column of cord; *r*, lateral tract of medulla continuous with, *c l*, the lateral column of the spinal cord.

the roots of these nerves deeply into the medulla, they are found to proceed to or from collections or columns of nerve-cells which lie in grey matter derived from the posterior cornu of the cord. They correspond then morphologically, and in a measure physiologically, to the

posterior roots of the spinal nerves, and their line of exit represents the postero-lateral groove of the cord and indeed is marked at first by a shallow sulcus continuous with that groove. If this line be traced upwards (fig. 261) it will be seen that the sulcus is obliterated or nearly so before long, so that the issuing bundles of nerve-roots alone serve to mark its position. As it passes upwards it becomes gradually more diverted from the middle line, turning outwards; so that opposite the place where the central canal opens into the calamus scriptorius of the fourth ventricle, the line in question has left the posterior surface and in the rest of its course runs along the lateral surface of the medulla. Towards the upper end it passes near the posterior margin of an oval prominence on the surface of the medulla termed the *olivary body* (*o*), but is separated from that prominence by a narrow tract. In transverse sections of the lower part of the medulla oblongata (fig. 262) it is seen that the bundles of fibres of the nerve-roots, in traversing the substance of the medulla to reach the grey matter near the central canal mark off a somewhat oval area on each side at the posterior part of the section. This area is termed by Flechsig the *posterior area of the medulla*, and the tracts of white fibres which can be traced, as will be immediately noticed, upon the surface of this part, may therefore be conveniently termed its *posterior columns*. They correspond in position to the posterior columns (posterior median column, and posterior lateral column) of the spinal cord.

The *line of origin of the anterior roots* of the spinal nerves is not marked in the spinal cord by a distinct furrow like that from which the posterior roots issue. But the same line, when traced upwards into the medulla, deepens into a well-marked longitudinal groove which is continued almost vertically as far as the lower border of the pons. In its upper part this groove separates the olivary prominence from the prominence of the pyramid. Just below the olivary body it is often obliterated for a certain part of its course by a band of transverse fibres. The root-bundles of the hypoglossal nerve (figs. 260, 261, *XII*) pass out from this furrow, and in transverse sections of the medulla they may be traced back through the substance of the organ to a group or column of nerve-cells situated in a portion of grey matter close to the antero-lateral side of the central canal in the lower closed part of the medulla (fig. 262), and close to the middle of the fourth ventricle in the upper opened-out part (fig. 268). This portion of grey matter is continuous below with part of the anterior cornu, so that the roots of the hypoglossal, both in their deep origin and in their place of exit, correspond with the anterior roots of the spinal nerves. In traversing the substance of the medulla they mark off an *anterior area*, wedge-shaped in transverse section, which is placed between them and the anterior median fissure (fig. 262, *f*). This area is on the surface marked by the prominence known as the *pyramid* or *anterior pyramid*, which corresponds in position (but only to a small extent in the fibres of which it is composed) with the anterior column of the spinal cord. The remainder of the transverse section of the medulla, after the posterior and anterior areas are deducted, lies between the line of nerve-root bundles of the hypoglossus and that of the successive bundles of the spinal accessory, vagus and glosso-pharyngeal. This is termed by Flechsig the *lateral area*, and on the surface it is marked below by a continuation of part of the lateral column of the cord, and above by the olivary prominence already alluded to.

We may now proceed to describe in detail the several parts which

appear upon the surface of the medulla in the three regions thus marked off by the two sets of nerve roots, commencing with the posterior columns.

Fig. 261.

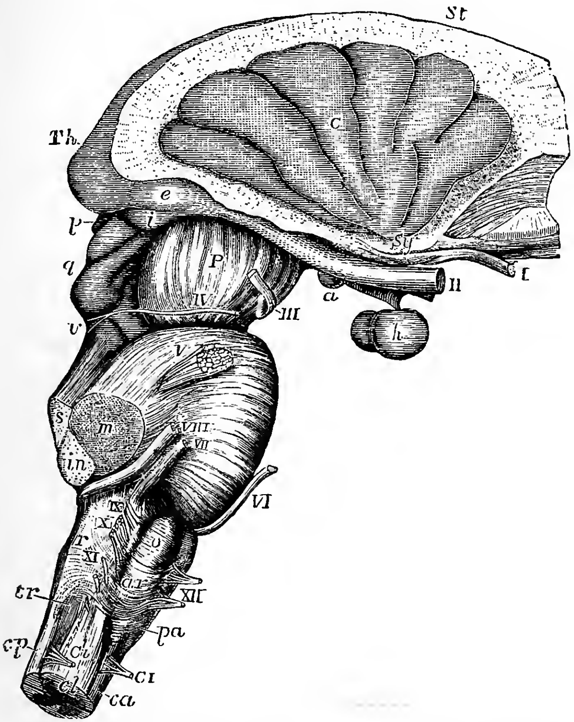


Fig. 261.—View of the medulla oblongata, pons Varolii, crura cerebri, and central parts of the encephalon from the right side. (Allen Thomson.)

The corpus striatum and thalamus opticus have been preserved in connection with the central lobe and crura cerebri, while the remainder of the cerebrum has been removed.

St, upper surface of the corpus striatum ; *Th*, back part of the thalamus opticus ; C, placed on the middle of the five or six convolutions constituting the central lobe or island of Reil, the cerebral substance being removed from its circumference ; *Sy*, fissure of Sylvius, from which these convolutions radiate, and in which are seen the white striæ of the olfactory tract ; I, the olfactory tract divided and hanging down from the groove in the convolution which lodges it ; II, optic nerves a little way in front of the commissure ; *a*, right corpus albicans with the tuber cinereum and infundibulum in front of it ; *h*, hypophysis or pituitary body ; *e*, external, and *i*, internal corpus geniculatum at the back part of the optic tract ; P, peduncle or crus of the cerebrum ; III, right oculo-motor nerve ; *p*, pineal gland ; *q*, corpora quadrigemina ; IV, trochlear nerve rising from *v*, the valve of Vieussens.

The following numbers and letters refer chiefly to parts in connection with the medulla and pons. V, placed on the pons Varolii above the right nervus trigeminus ; *s*, the superior, *m*, the middle, and *in*, the inferior peduncle of the cerebellum cut short ; VI, the sixth nerve ; VII, facial nerve ; VIII, auditory nerve ; IX, the glosso-pharyngeal nerve ; X, placed opposite to the cut end of the pneumo-gastric nerve ; and XI, the uppermost fibres of the spinal accessory nerve ; XII, the hypoglossal nerve ; *p a*, pyramid ; *o*, olive ; *a r*, arciform fibres ; *r*, restiform body ; *tr*, tubercle of Rolando ; *c a*, anterior, *c p*, posterior, and *c l*, lateral columns of the spinal cord ; *C I*, *C i*, anterior and posterior roots of the first cervical nerve.

Fig. 262.

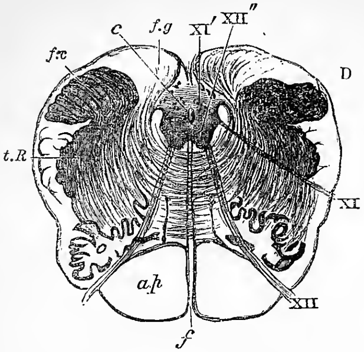


Fig. 262.—SECTION ACROSS THE MEDULLA OBLONGATA A LITTLE BELOW THE POINT OF THE CALAMUS SCRIPTORIUS (Lockhart Clarke).

c, central canal; *f*, anterior median fisssure; *f.g.*, funiculus gracilis; *f.c.*, funiculus cuneatus; *t.R*, tubercle of Rolando; *o*, olivary body; *a.p*, pyramid; XI, XII, spinal accessory and hypoglossal nerves; XI′, XII′, their nuclei.

Posterior columns. It will be remembered that in the upper region of the spinal cord a small portion of the whole posterior column is marked off from the rest by a well-developed pia-matral septum, and is indicated in the surface by a distinct longitudinal prominence bounded laterally by a shallow groove. The portion thus marked off is the posterior

Fig. 263.

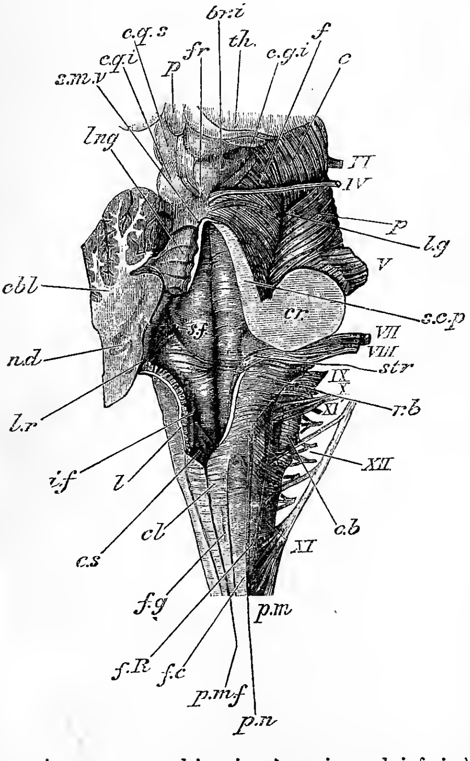


Fig. 263.—POSTERIOR AND LATERAL VIEW OF THE MEDULLA OBLONGATA, FOURTH VENTRICLE AND MESENCEPHALON (E.A.S.). NATURAL SIZE.

The cerebellum and inferior medullary velum, and the right half of the superior medullary velum, have been cut away, so as to expose the fourth ventricle.

p.n., line of the posterior roots of the spinal nerves; *p.m.f.*, posterior median fissure; *f.g.*, funiculus gracilis; *cl.*, its clava; *f.c.*, funiculus cuneatus; *f.R.*, funiculus of Rolando; *r.b.*, restiform body; *c.s.*, lower end of the fourth ventricle (calamus scriptorius); *l*, section of the ligula or tænia; part of the choroid plexus is seen beneath it; *l.r.*, lateral recess of the ventricle; *str.*, striæ acusticæ; *i.f.*, inferior (posterior) fovea; *s.f.*, superior (anterior) fovea; between it and the median sulcus is the funiculus teres; *cbl.*, cut surface of the left cerebellar hemisphere; *n.d.*, central grey matter (nucleus dentatus) seen as a wavy line; *s.m.v.*, superior (anterior) medullary velum; *lng.*, lingula; *s.c.p.*, superior cerebellar peduncle cut longitudinally; *cr.*, combined section of the three cerebellar peduncles (the limits of each are not marked); *c.q.s.*, *c.q.i.*, corpora quadrigemina (superior and inferior); *fr.*, frænulum; *f*, fibres of the fillet, seen on the surface of the tegmentum; *c*, crusta; *l.g.*, lateral groove; *c.g.i.*, corpus geniculatum internum; *th.*, posterior part of thalamus; *p*, pineal body. The roman numbers indicate the corresponding cranial nerves.

median column, and the prominence, which is continued up into the medulla oblongata becomes there still better marked, and is known as the *funiculus gracilis* (fig. 263, *f. g*). This, as it is traced upwards, especially as the fourth ventricle is approached, broadens out into an expansion termed the *clava*(*cl.*), and as the ventricle opens out the clavæ of opposite sides diverge and form the lateral boundary to the ventricle in its lower part. Above, the clavæ are tapered off and soon become no longer traceable.

The funiculi graciles with their clavæ are sometimes described as the *posterior pyramids.*

Between the posterior median column and the postero-lateral groove from which the posterior roots of the cervical nerves pass out there is found in the upper part of the cord a single distinct column, viz., the posterior lateral column. This is also the condition at the lowest part of the medulla close to its junction with the cord. But very soon there begins to be interpolated between the prolongation of this column and the groove in question another longitudinal prominence which is at first narrow but soon broadens out into a considerable eminence known as the *tubercle of Rolando.* The longitudinal prominence which passes up into it, is termed therefore by Schwalbe, the *funiculus of Rolando* (fig. 263, *f.R.*). What may be regarded as the prolongation of the posterior lateral column also gradually expands as it ascends, so that it has a somewhat wedge-like form and it is accordingly known as the *cuneate funiculus* (*f.c.*). On a level with the adjoining clava of the funiculus gracilis, the enlarged part of the cuneate funiculus also, like that, exhibits a slight eminence, which is best marked in children, and has been termed the *cuneate tubercle* (Schwalbe). Beyond this the cuneate funiculus passes the clava, and assists in forming the lateral boundary of the fourth ventricle.

The funiculus of Rolando is termed by Henle the lateral cuneate funiculus ; it is produced, as we shall presently see, by the approach of the caput cornu posterioris to the surface.

In the upper part of the medulla oblongata, the cuneate funiculus is concealed by a set of fibres (*external arciform or arcuate fibres*) which issue from the anterior median fissure and passing transversely outwards on the surface of the anterior pyramids and olivary body, turn upwards to join the restiform body. There is also a narrow strand of fibres marked by its white appearance which crosses the line of the posterior roots from the lateral column, just above the level of the tubercle of Rolando, and joins this tract of oblique fibres. This is the *lateral cerebellar tract* which has been already noticed in the description of the spinal cord. These obliquely crossing fibres turn upwards as they cross the funiculus of Rolando and cuneate funiculus, and appear to blend with them to form a rounded prominent cord, the *corpus restiforme* or rope-like body (fig. 263, *r. b.*) which passes directly into the corresponding hemisphere of the cerebellum, constituting its inferior peduncle.

The term "restiform body" is sometimes made to include the whole of the posterior column of the medulla, with the exception of the funiculus gracilis, but with the addition of the lateral cerebellar tract, and the fibres which cross as above noticed from the anterior pyramids. By others again the term is used synonymously with the posterior column. But it is more convenient to employ it in the restricted sense to indicate the tract of the medulla which passes up

into the cerebellum, and this is mainly constituted as will be presently seen by the arched fibres above mentioned, reinforced by the lateral cerebellar tract; the fibres in the cuneate funiculus and funiculus of Rolando being in all probability not continued up into the cerebellar peduncle, as from the surface those funiculi sometimes appear to be.

Fig. 264.

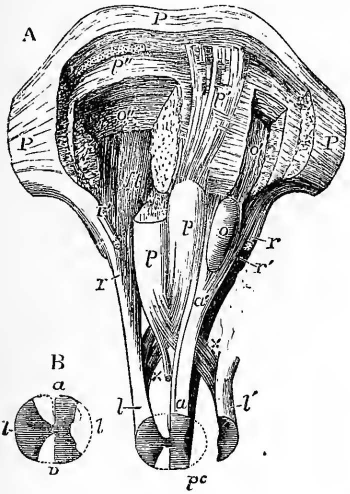


Fig. 264.—Dissection of the medulla oblongata and pons showing the course of the pyramidal tracts in them. (Allen Thomson.)

P, pons Varolii; *p*, the pyramids, the upper part of the right one has been cut away; *p'*, the fibres of the left pyramid, as they ascend through the pons, exposed by the removal of the superficial transverse fibres; *p''* is placed on some deeper transverse fibres of the pons on the right side, below the divided fibres of the right pyramid; *a*, left anterior column of the cord, its median part passes upwards into the outer part of the pyramid, the remainder dips beneath the pyramid and olivary body; *o*, olivary body; *o'*, the continuation of part of the lateral column ascending through the pons and exposed by the removal of a small portion of the deeper transverse fibres; *o''*, some of the same fibres divided by a deeper incision on the right side; *l*, *l'*, the lateral columns of the cord; ×, their deeper parts passing by decussation into the pyramids; *r*, direct cerebellar tract passing from the lateral column into the inferior peduncle of the cerebellum, or restiform body; *r'*, fasciculus passing from the anterior column to the same; *ft*, deep longitudinal fibres derived from the anterior and lateral columns of the cord.

B, explanatory outline of the section of the spinal cord. *a*, anterior columns; *p*, posterior; *l*, lateral.

Lateral columns.—The lateral column of the spinal cord appears, on the surface, to be directly continued upwards into the lateral column of the medulla oblongata. In reality, however a considerable tract of the white fibres—that which in the spinal cord we have noticed as the lateral pyramidal tract—is found, at the lower end of the medulla, to cross obliquely in stout bundles through the grey matter of the anterior cornu, and across the anterior median fissure to the other side of the medulla, where they form the mesial and larger part of the pyramid. The rest of the lateral column can be traced vertically upwards (with the exception of the lateral cerebellar tract which passes, as already indicated, backwards into the restiform body) as far as the lower end of the olive where its longitudinally coursing fibres become concealed by this prominence and by the arched fibres already noticed.

The **olivary body** (figs. 260, 261, *o*) is, as its name implies, an olive-shaped prominence, which lies in the upper part of the medulla immediately above the apparent termination of the lateral column, and extending nearly as far as the lower border of the pons, being only separated from this by a deep groove in which is sometimes a small band of arched fibres. The line of exit of the hypoglossal nerve-roots lies on its inner or mesial border, that of the accessory, vagus and glossopharyngeal roots along its outer side, but the latter are separated from it by a groove in

which longitudinal fibres prolonged from the lateral tract can be seen. Sometimes there is a small longitudinal tract running along its inner border also, and in such case, with the arched fibres above and below, the olive appears to be entirely enclosed by a fibrous strand, which has sometimes been described as its capsule (*siliqua olivæ*). The longitudinal tracts before and behind the olive are often concealed in great measure by the arched fibres, which may form a complete superficial layer over the olive, and indeed over the whole anterior and lateral surface of this upper part of the medulla.

Anterior columns. Pyramids of the medulla.—The anterior columns of the cord, although on superficial inspection they appear to be prolonged into the pyramids of the medulla, are so only to a small extent. For the lateral pyramidal tract, crossing the anterior median fissure from the lateral column, is continued upwards close to that fissure, and unites with the comparatively small anterior pyramidal tract to constitute the prominence known as the *pyramid.* The prolongation upwards of the rest of the anterior column of the cord lies deeply, being altogether concealed from view by the pyramids.

The **pyramids** (fig. 260, *pa*), are broader and more prominent above than below. They are bounded internally or mesially by the anterior median fissure, and externally by the olivary bodies, being separated from these by the groove before mentioned, from which the roots of the hypoglossal nerve issue. At their upper end they are constricted, and thus enter the substance of the pons, through which their fibres may be traced into the peduncles of the cerebrum.

Fig. 265.

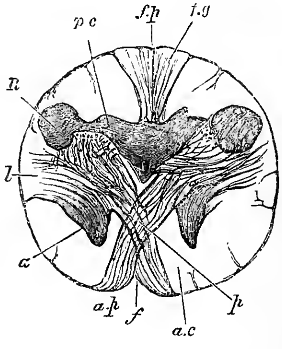


Fig. 265.—Section of the medulla oblongata at the middle of the decussation of the pyramids (Lockhart Clarke).

f, anterior; *f.p.*, posterior fissure; *a.p.*, pyramid; *a*, remains of part of anterior cornu, separated by the crossing bundles from the rest of the grey matter; *l*, continuation of lateral column of cord; *R*, continuation of substantia gelatinosa of Rolando; *p.c.*, continuation of posterior cornu of grey matter; *f.g.*, funiculus gracilis.

The *decussation of the pyramids* is the name given to the obliquely crossing bundles of the lateral pyramidal tract which are seen in the anterior median fissure at the lower part of the medulla. The extent to which the decussation is visible varies considerably in different individuals; for in some the bundles take a deeper, in others a more superficial course. Further, in some cases a larger share than usual of the longitudinal fibres of the pyramids passes down in the anterior pyramidal tract and a correspondingly smaller share in the lateral pyramidal tract. And since the anterior tract, which in the pyramid is external to the lateral tract, does not cross in the medulla but merely passes obliquely at its lower end to attain the side of the anterior median fissure, the decussation in these cases is of less extent. On the other hand, in rare cases, the whole of the fibres of the anterior pyramid may cross over at the lower part of the medulla and become lateral pyramidal tract, in which case the anterior or uncrossed tract is wanting in the

cord, and the medullary decussation is very well marked. All transitions are found between these two conditions (see p. 278).

Medullary portion of the fourth ventricle.—The external characters of the medulla oblongata may be completed by a description of that part of it which enters into the formation of the floor of the fourth ventricle. This is the space into which the central canal of the cord, after becoming somewhat enlarged and cleft-like, opens out on the posterior or dorsal aspect of the medulla (fig. 263). The opening-out seems as if effected by the divergence of the funiculi graciles on either side at an acute angle, but the lateral boundaries of the ventricle curve round with their convexity towards the ventricle, and the latter rapidly broadens, so that opposite the middle peduncle of the cerebellum it has attained its greatest width. From this point its upper part again narrows, converging gradually above to be continued into the comparatively narrow Sylvian aqueduct. The ventricle is therefore irregularly lozenge- or diamond-shaped, and is sometimes named *fossa rhomboidalis*. The pointed lower end of the ventricle has the shape of a writing pen, and is termed the *calamus scriptorius* (fig. 266). At its widest part the fourth ventricle is continued for a short distance on either side between the cerebellum and medulla where these come in contact, in the form of the pointed *lateral recess* (*l.r.*). The lateral boundaries of the ventricle in its lower or medullary part are the clavæ of the funiculi graciles, the funiculi cuneati, and the restiform bodies. The roof or posterior wall is formed by a simple layer of flattened epithelium covered by pia mater; but it is not quite complete, for there is a hole in it termed the *foramen of Majendie* a little above the place where the central canal opens out into the ventricle, and there are two other apertures in the epithelial roof in the lateral recesses just mentioned.

Fig. 266.

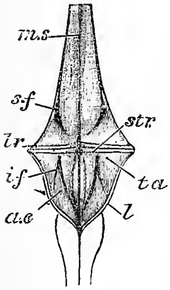


Fig. 266.—Anterior boundary (floor) of the fourth ventricle (E.A.S.). Natural size.

m.s., median sulcus; *str.*, striæ acusticæ, marking the limit between the upper part of the ventricle and the lower medullary part or calamus scriptorius; *l.r.*, lateral recess; *i.f.*, inferior (posterior) fovea; *a.c.*, ala cinerea; *t.a.*, acoustic tubercle; *s.f.*, superior (anterior) fovea, close to the lateral margin of the anterior part of the ventricle.

At the sides and below, this layer of epithelium passes into continuity with the epithelium covering the floor, but it is somewhat thickened by the addition of white nervous matter before reaching the lateral boundaries of the floor. This thickening is left as a slightly prominent and often ragged membrane when the epithelium of the roof of the ventricle is torn off with the pia mater. It commences at the apex of the clava, and accompanies the lateral boundary for a short distance; then turns over the surface of the restiform body and terminates close to the place from whence the roots of the vagus and glosso-pharyngeal nerves issue. It is termed the *tænia* or *ligula* (figs. 263, 266, *l*), and its upper transverse part forms the lower boundary of the lateral recess of the ventricle. Another thickening in the epithelial membrane is sometimes seen at the apex of the ventricle roofing over the point of the calamus scriptorius: this is named the *obex*.

Two longitudinal vascular inflexions of the pia mater, known as the choroid plexuses of the 4th ventricle, project from the roof into the

cavity on either side of the middle line, covered everywhere, however, by the epithelium of the roof. Offsets from these pass also into the lateral recesses (fig. 263), from the apices of which they emerge, encircled by a duplicature of the ligula, which was termed by Bochdalek the *cornucopia.* The epithelial layer of the roof of the ventricle follows all the convolutions of the choroid plexuses, but is nowhere pierced by them; it is generally described as the epithelium of the plexuses.

The part of the floor of the 4th ventricle which belongs to the description of the medulla oblongata is marked off superiorly by some transverse white lines, which cross the grey matter of the floor, and are known as the *striæ medullares seu acusticæ* (fig. 266, *str*). These arise close to the median line, and curve outwards over the restiform bodies to join the roots of the auditory nerve. They sometimes form a tolerably compact bundle, sometimes are more separate from one another, and occasionally are not to be made out on the surface, probably in these cases having a deeper course.

This lower and smaller part of the floor of the ventricle is bisected by a slight median groove. A little on either side of this groove and immediately below the striæ medullares, is a small triangular depression (*inferior fovea,* fig. 266, *i.f.*), the apex of which extends only as far as the striæ, but the base is prolonged into two grooves extending one from each angle. The inner of the two grooves passes with a slightly curved course towards the point of the calamus scriptorius, and thus cuts off a pointed triangular area), which is bounded mesially by the median sulcus, and the base of which is turned towards the striæ acusticæ. This area is slightly prominent, and constitutes the lower end of what will presently be described as the fasciculus teres; in it is the prolongation of the tract of nerve-cells from which the roots of the hypoglossal nerve take origin. The groove which is prolonged from the outer angle of the fovea, passes downwards with a slight outward obliquity nearly to the lateral boundary of the ventricle, and marks off externally another triangular area, the base of which is also directed upwards, where it can be traced into a prominence, (best marked in children) over which the striæ acusticæ course (*t.a.*). To this prominence Schwalbe has given the name *tuberculum acusticum,* since the main part of the auditory nerve arises in connection with it and with the triangular lateral area behind.

Included between the two grooves is a third triangular area, the apex of which is at the inferior fovea, while its base looks downwards and outwards. This area has a distinctly darker colour than the rest of the floor of the ventricle, and especially than the funiculi teretes on the inner side, which have a whitish grey appearance, and it has accordingly been named the *ala cinerea* (*a.c.*). Towards the apex it is somewhat depressed, but below it is elevated into a distinct prominence (*eminentia cinerea*). It contains the nucleus of the vagus, and superiorly, near the fovea, of the glosso-pharyngeal nerve.

INTERNAL STRUCTURE OF THE MEDULLA OBLONGATA.

The internal structure of the medulla, like the external form, will be best understood by tracing its several parts upwards from the spinal cord; and this can be most readily done by a comparison of the appearances of successive transverse sections.

The first changes are produced, both in internal structure and in the external form, by the passage of the fibre-bundles of the lateral pyramidal tract obliquely through the grey matter of the anterior cornu, and across the anterior median fissure to the pyramid of the opposite side (fig. 265). By this abrupt passage of a large number of white fibres through it, the anterior cornu is broken up, and one part, the caput cornu (*a*), is entirely separated from the rest of the grey matter; whilst only the base of the cornu remains, as a small portion of grey matter close to the antero-lateral aspect of the central canal.

The separated portion of the anterior cornu becomes pushed over to the side by the development of the pyramid and the interpolation higher up of the olivary body between them, so that it comes to lie close to the remains of the posterior cornu (see below). The greater part of its substance is broken up into a *formatio reticularis* (fig. 267, *f.r.*), *i.e.* a comparatively coarse network of grey matter containing nerve-cells, intersected by bundles of white fibres; but a small part of the cornu remains for a time in the lateral column, near the surface, and is known as the nucleus of that column (*nucleus lateralis*, (fig. 267, *n.l.*)).

Meanwhile the posterior cornua become gradually shifted laterally, simultaneously with an increase in size of the posterior columns of the

Fig. 267.

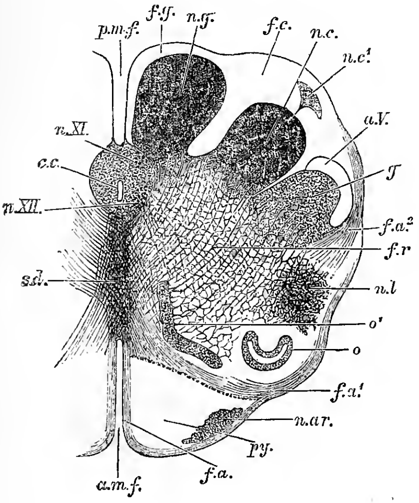


Fig. 267. Section of the Medulla Oblongata in the Region of the Superior Pyramidal Decussation. (Schwalbe.) $\frac{4}{1}$

a.m.f., anterior median fissure; *f.a.*, superficial arciform fibres emerging from the fissure; *py.*, pyramid; *n.ar.*, nucleus of the arciform fibres; *f.a'.*, deep arciform fibres becoming superficial; *o.*, lower end of olivary nucleus; *o'.*, accessory olivary nucleus; *n.l.*, nucleus lateralis; *f.r.*, formatio reticularis; *f.a.*^{2}, arciform fibres proceeding from formatio reticularis; *g.*, substantia gelatinosa of Rolando; *a.V.*, ascending root of fifth nerve; *n.c.*, nucleus cuneatus; *n.c'.*, external cuneate nucleus; *f.c.*, funiculus cuneatus; *n.g.*, nucleus gracilis; *f.g.*, funiculus gracilis; *p.m.f.*, posterior median fissure; *c.c.*, central canal surrounded by grey matter, in which are, *n.XI.*, nucleus of the spinal accessory, and, *n.XII.*, nucleus of the hypoglossal: *s.d.*, superior pyramidal decussation.

medulla, so that in place of forming an acute angle with the posterior median fissure, they now lie almost at right angles to it (fig. 265). Moreover, the caput cornu enlarges and comes close to the surface, where it presently forms a distinct projection, the funiculus of Rolando, which, a little higher up, swells into the tubercle of Rolando (fig. 265, R.). At the same time the cervix cornu diminishes in size and like the anterior cornu is eventually broken up by the passage of transverse and longitudinal bundles of white fibres through it, into a reticular formation, which then separates the caput cornu posterioris (fig. 267, *g.*) from the

rest of the grey matter, and joins the reticular formation derived from the anterior cornu. In the tubercle of Rolando the caput cornu is close to the surface, and its grey substance can readily be seen, but above the tubercle it lies deeper, being covered by a well-marked bundle of ascending white fibres (ascending root of the 5th nerve (*a. V.*)) and by the oblique arched fibres which are passing over it to form the restiform body.

The grey matter of the base of the posterior cornu undergoes a considerable increase as we trace it upwards in sections. For portions of grey matter are soon found to extend from it into the funiculi graciles and cuneati, forming the so-called nuclei of those columns (figs. 267, 268, *n.g.*, *n.c.*). These nuclei are at first narrow in transverse section;

Fig. 268.

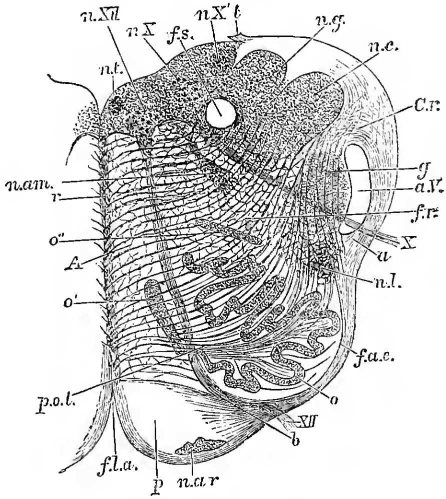


Fig. 268. SECTION OF THE MEDULLA OBLONGATA AT ABOUT THE MIDDLE OF THE OLIVARY BODY. (Schwalbe.) $\frac{4}{1}$

f.l.a., anterior median fissure; *n.ar.*, nucleus arciformis; *p.*, pyramid; *XII.*, bundle of hypoglossal nerve emerging from the surface; at *b*, it is seen coursing between the pyramid and the olivary nucleus, *o.*; *f.a.e.*, external arciform fibres; *n.l.*, nucleus lateralis; *a.*, arciform fibres passing towards restiform body partly through the substantia gelatinosa, *g.*, partly superficial to the ascending root of the 5th nerve, *a. V.*; *X.*, bundle of vagus root, emerging; *f.r.*, formatio reticularis; *c.r.*, corpus restiforme, beginning to be formed, chiefly by arciform fibres, superficial and deep; *n.c.*, nucleus cuneatus; *n.g.*, nucleus gracilis; *t.*, attachment of the ligula; *f.s.*, funiculus solitarius; *n.X.*, *n.X′.*, two parts of the vagus nucleus; *n.XII.*, hypoglossal nucleus; *n.t.*, nucleus of the funiculus teres; *n.am.*, nucleus ambiguus; *r.*, raphe; *A.*, continuation of anterior column of cord; *o′*, *o″*, accessory olivary nuclei; *p.o*, pedunculus olivæ.

but as the central canal approaches the posterior surface of the medulla they appear as comparatively thick masses, which produce externally the eminences of the clava and the cuneate tubercle. Outside the nucleus of the funiculus cuneatus (which is often known as the restiform nucleus) a small accessory or external nucleus becomes formed (fig. 267, *n.c′.*).

When the slit-like upper end of the central canal opens out into the 4th ventricle, the small remaining portion of the base of the anterior cornu comes to the surface of the floor of the ventricle, and as the sections are traced forward increases gradually in size, producing the eminence of the funiculus teres. In it, both in the lower part of the medulla where the canal is still closed and above where it has opened out, a group of large nerve-cells (*n.XII.*) is seen in the transverse sections, representing a longitudinal vesicular column. From this column of cells the successive bundles of the roots of the hypoglossal or 12th cranial nerve arise and pass obliquely through the substance of the medulla to

leave it on its anterior aspect. The tract of nerve-cells is accordingly known as the **hypoglossal nucleus.**

In the 4th ventricle the hypoglossal nucleus lies a short distance from the surface. Nearer to the surface of the floor and nearer also to the median groove is a small group of cells continuous with those found in the raphe, presently to be described, and known sometimes as the nucleus of the funiculus teres (fig. 268, *n.t.*).

At the base of the posterior cornu in the lower part of the medulla, and near the central canal, a group of cells (fig 267, *n. XI.*) is seen in section, which seems to correspond with the hypoglossal group in the base of the anterior cornu. This, if traced upwards, is found to be pushed to the side as the central canal opens, so that in the floor of the ventricle it lies outside the hypoglossal nucleus (fig. 268, *n.X.*). The group or column of cells in question corresponds to the prominence of the ala cinerea which appears on the surface, and it extends forwards as far as the fovea posterior. From it there arise successively bundles of fibres of the roots of the spinal accessory, vagus and glosso-pharyngeal nerves (11th, 10th, and 9th cranial nerves) : those of the upper roots of the spinal accessory in the lower part of the medulla where the canal is still closed ; those of the vagus beginning at the commencement of the ventricle, and arising along the length of the eminentia cinerea ; and those of the glosso-pharyngeal coming for the most part from the upper part of the ala cinerea, and from the posterior fovea. The column of cells in question forms then successively the **nucleus of the spinal accessory, pneumogastric and glosso-pharyngeal nerves.**

Fig. 269.

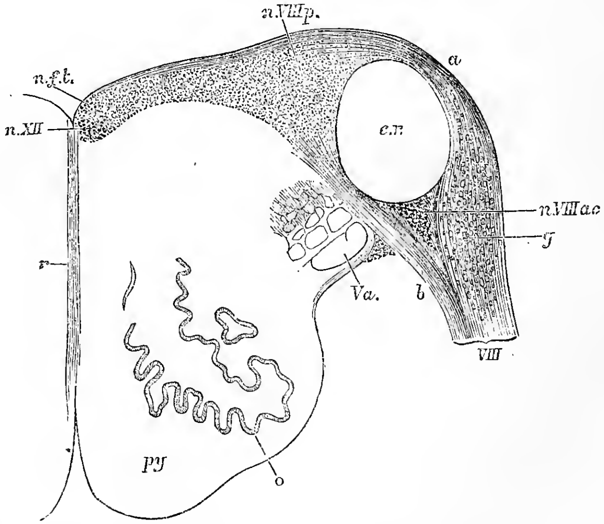


Fig. 269. Transverse section of the upper part of the medulla oblongata. (Schwalbe.) $\frac{4}{1}$

py., pyramid ; *o.*, olivary nucleus ; *V.a.*, ascending root of the fifth nerve ; *VIII.*, inferior (posterior) root of the auditory nerve, formed of two parts, *a.* and *b.*, which enclose the restiform body, *c.r.* ; *n. VIII.p.*, principal nucleus of the auditory nerve ; *n. VIII.ac.*, accessory nucleus ; *g.*, ganglion cells in the root ; *n.f.t.*, nucleus of the funiculus teres ; *n.XII.*, nucleus of the hypoglossal ; *r.*, raphe.

Towards the upper part of the medulla another tract of cells becomes developed outside the line of the accessory, vagus, and glosso-pharyngeal nuclei. This tract corresponds to the lateral triangular area which is seen on the surface outside the ala cinerea, and which passes into the tuberculum acusticum of Schwalbe. From it most of the fibres of the 8th or auditory nerve take origin, and it is accordingly named the **principal auditory nucleus.**

The nerve-cells in the hypoglossal nucleus are larger than those in the spinal accessory, vagal and glossopharyngeal nuclei. Those in the nucleus of the funiculus gracilis are also of considerable size.

Nucleus of the Olivary Body.—Besides those collections of grey matter which are traceable from the grey matter of the spinal cord, portions occur in certain parts of the medulla oblongata, which are not represented in the cord. Of these the most important is the *nucleus of the olivary body*, which has been termed, from its appearance in section, the *corpus dentatum of the olive* (fig. 268, *o*). It is enclosed in the olivary prominence, and is therefore situated in the lateral area of the medulla, but the grey matter is not visible from the surface, being covered by both longitudinal and transverse white fibres. It takes the form of a thin wavy lamina, which is curved round at its edges so as to form an ovoid scalloped capsule. The open part or hilus of this looks towards the middle line and receives a considerable tract of white fibres, which emanate from the anterior area immediately behind the pyramid, and pass into the hilus along its whole extent, forming the so-called *olivary peduncle* (*p.o.*). Under the microscope the nucleus appears as a wavy band of neuroglia, with small multipolar nerve-cells embedded in it. The fibres of the olivary peduncle diverge as they pass to the grey lamina. They partly terminate in the axis-cylinder processes of its cells, and partly pass in small bundles through the lamina, those which are more posterior turning backwards and coursing obliquely (as internal arcuate fibres) through the posterior part of the lateral area to join the restiform body, whilst the others have a more direct course through the grey lamina and run between the longitudinal fibres which cover the olive. On reaching the surface they bend round and are continued as part of the layer of external arcuate fibres. Some may not reach the surface, but turn upwards and reinforce the longitudinal fibres just mentioned.

Besides the main olivary nucleus two smaller isolated bands are generally seen (figs. 267, 268, *o′*, *o″*), looking like separated portions of the chief nucleus. They are situated one on the dorsal, and the other on the mesial aspect of the chief nucleus, and are known as the outer and inner *accessory olivary nuclei.* They are traversed like the main nucleus by bundles of internal arcuate fibres going to the restiform body, and are frequently connected at one or two places to the main nucleus. The inner accessory nuclei are sometimes termed the pyramidal nuclei, for they lie immediately behind the pyramid. The root-bundles of the hypoglossal nerves generally pass between them and the chief olivary nucleus after traversing the olivary peduncle, but sometimes the nerve pierces the chief nucleus near its mesial edge.

Other small collections of grey matter and nerve-cells are scattered in certain parts of the formatio reticularis, as well as one or two distinct tracts in connection with the external arcuate fibres, and a considerable amount in the median septum or raphe. These three structures may therefore next be described.

The **formatio reticularis** (figs. 267, 268, *f.r.*) occupies the whole of the anterior and lateral areas of the medulla, dorsal to the pyramids and olives respectively. It is thus named on account of the appearance which it presents in a transverse section viewed under a moderate magnifying power (fig. 270). This reticular appearance is caused by the intersection of bundles of fibres belonging to two sets which run at right angles

Fig. 270.

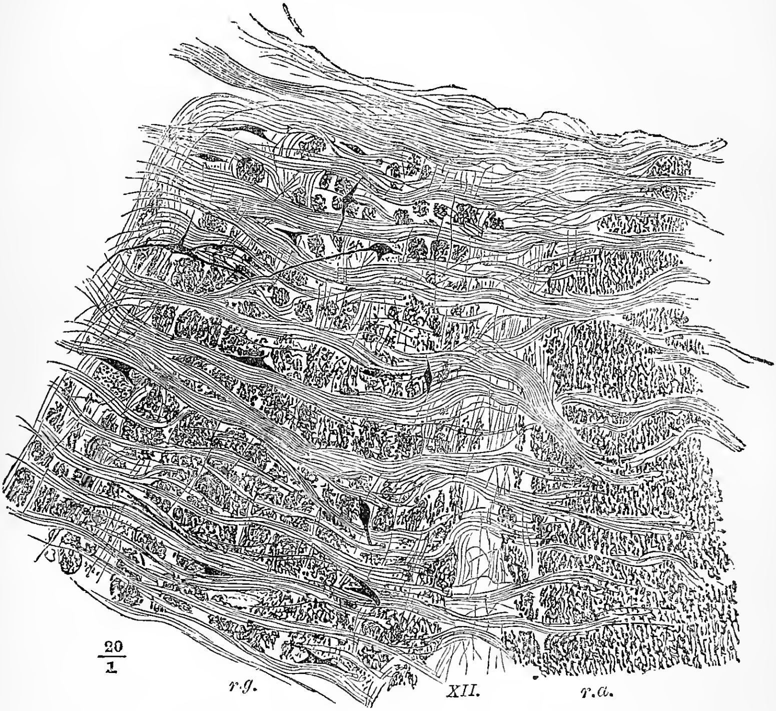


Fig. 270.—Part of the reticular formation of the medulla oblongata (Henle).

r.a., reticularis alba; *r.g.*, reticularis grisea; between them a root-bundle of the hypoglossus (*XII*). The longitudinal fibres of the reticular formation are cut across; the transversely coursing fibres are internal arcuate fibres, passing on the right of the figure towards the raphe.

to one another. Those of the one set are longitudinal, and these are intersected by transverse fibres, which pass obliquely from the raphe outwards and somewhat backwards with a curved course towards the funiculus gracilis and funiculus cuneatus, and the olivary nucleus; and also in the upper part of the medulla, towards the restiform body.

In some parts grey matter with nerve-cells enters into the constitution of the formatio reticularis. The cells are especially large and numerous in the reticular formation of the lateral area near the remains of the anterior cornu; and its grey matter is presumably derived in great

measure from the latter. In the anterior or mesial area of the medulla, nerve-cells are absent from the formatio reticularis, and this is therefore sometimes distinguished as the *formatio reticularis alba* (fig. 270, *r.a.*), from the other or *formatio reticularis grisea* (*r.g.*).

The longitudinal fibres of the reticular formation of the anterior area (with the exception of those which occupy the tract nearest to the pyramids), are prolonged from the remainder of the anterior column of the spinal cord after the passage of the anterior (direct) pyramidal tract into the outer side of the pyramid. Those nearest the pyramids are derived from arched fibres which issue from the nuclei of the funiculi graciles and from the olives, and turn longitudinally upwards in this part. Those of the reticular formation of the lateral area are prolonged from the remains of the lateral column after the lateral pyramidal tract and the lateral cerebellar tract have passed to their respective destinations. They are added to as we trace them upwards in sections, the increase being due either to the turning upwards of some of the inner curved fibres, or to the accession of fibres which are derived from nerve-cells in the grey matter near the posterior surface, or in the grey reticular formation.

According to Deiters, the axis-cylinder processes of the nerve-cells of the reticular formation all pass downwards, while their branched processes are directed horizontally.

The **arciform or arcuate fibres** of the medulla, which have been more than once alluded to, are the curved fibres which are seen in transverse sections coursing in the plane of the section. From their position they are distinguished into external and internal, or superficial and deep.

The *superficial arcuate fibres* (*f.a.e.* in fig. 268) emerge for the most part from the anterior median fissure, and passing over the pyramids and olives, many of them go to the restiform body. They are added to by deep fibres which come to the surface partly in the groove between the pyramids and olives, partly after passing through the olives, as before mentioned. Traced back in the anterior median fissure they are seen to enter the raphe, and to cross over in it; after which it is supposed that they may become longitudinal, but their further course is not certainly known.

The *deep arcuate fibres* emerge from the raphe, and traverse the thickness of the medulla, tending towards the olives, the restiform body, and the nuclei of the cuneate and slender funiculi. As we have just seen, those which pass through and in front of the olives are in continuity with the superficial arcuate fibres.

Traced backwards into the raphe, the deep arcuate fibres appear to cross obliquely to the other side of the medulla, where in all probability they mostly become longitudinal, joining the fibres of the formatio reticularis alba. Others are said to turn upwards and become longitudinal before reaching the raphe. The cells of the formatio reticularis grisea are probably connected with some of the deep arcuate fibres.

Nuclei of the superficial arcuate fibres.—Amongst the superficial arcuate fibres, or between them and the subjacent columns of the medulla, small collections of grey matter with nerve-cells are here and there met with, which are distinguished by the above name. The principal group of cells lies superficial to the pyramid on either side (figs. 267, 268, *n.ar.*). The nerve-cells of these nuclei are connected partly with the arciform fibres, partly with the fibres of the adjacent pyramid.

The **raphe** or septum (fig. 268, *r*) is composed of fibres which run in part dorso-ventrally (fibræ rectæ), in part longitudinally, and in part

across the septum more or less obliquely. Intermixed amongst the nerve-fibres are a number of nerve-cells in grey matter. The fibræ rectæ are continuous anteriorly with the superficial arched fibres, which emerge at the anterior median fissure; posteriorly with fibres from the funiculi graciles in the lower part, and from the nuclei of the funiculi teretes in the upper part of the medulla. The longitudinal are chiefly fibres which have passed into the raphe as fibræ rectæ or as superficial or deep arcuate fibres, and in it have altered their direction and become longitudinal. The obliquely crossing fibres are the deep arched fibres which enter or emerge from the raphe. Others, however, near the dorsal edge of the raphe seem to come from the nuclei of the nerve-roots, and these may pass more directly across as commissural fibres either into the formatio reticularis or into the pyramid of the other side, in either case becoming longitudinal. The nerve-cells of the raphe are multipolar cells, those in the middle being chiefly spindle-shaped. The latter are connected with fibræ rectæ (Clarke), whilst the more laterally situated ones, at least those near the anterior median fissure, are connected with some of the superficial arcuate fibres.

Course of nerve-fibres from the spinal cord upward through the medulla oblongata.—Assuming for convenience of description the existence of three white columns of the spinal cord on each side, the various parts of these are continued upwards as follows :—

The *posterior column* forms in the medulla oblongata the white substance of the three posterior funiculi; viz. the f. gracilis, f. cuneatus and f. Rolandi. The longitudinal fibres of the first two appear to end in the grey matter which forms their nuclei; and numerous deep arcuate fibres enter or emerge from the same collections of grey matter.

The cuneate funiculus, has been commonly described as passing up into the restiform body, but it seems doubtful if any of its fibres do actually take part in the constitution of that body, although from the surface the funiculus in question and the restiform body appear to be in continuity with one another.

A large part of the *lateral column* of the cord, viz., the *lateral pyramidal tract* (fig. 264, ×), passes into the opposite pyramid of the medulla and ascends in this and in the ventral half of the pons towards the peduncle of the cerebrum. Together with the small part of the anterior column of the cord which also enters into the constitution of the pyramid, it forms the *pyramidal tract of the encephalic isthmus* of Flechsig (peduncular tract of Meynert). Some of the fibres of the pyramid, however, emerge as external arcuate fibres, and joining the restiform body pass to the cerebellum. A smaller part of the lateral column of the cord, the *direct lateral cerebellar tract* (fig. 264, *r*), passes at about the middle of the medulla obliquely backwards to join the restiform body.

The rest of the lateral column dips under the olives and forms the longitudinal fibres of the reticularis grisea. These are continued through the dorsal parts of the encephalic isthmus towards the corpora quadrigemina and optic thalamus.

The *anterior column* of the cord (fig. 264, *a*) in part is continued into the pyramid of the same side, but chiefly dips under the pyramid and forms the longitudinal fibres of the reticularis alba in the dorsal part of the mesial area. These pass upwards towards the cerebrum. In the pons Varolii one tract of them becomes collected into a well marked fasciculus

(posterior longitudinal bundle), and most of the others form another tract (tract of the fillet) which terminates in the region of the corpora quadrigemina; the further destination of these will be afterwards noticed. In the region of the medulla, they are indistinguishable from one another in the adult, but in the fœtus they are found to develope at different periods and are then readily differentiated (Flechsig).

A small bundle of fibres of the anterior column of the cord was described by Solly as passing obliquely upwards below the olive, to join the restiform body. This is not always present.

THE CEREBELLUM AND PONS.

The part of the encephalon which lies next above the medulla oblongata encircles the upper part of the fourth ventricle. Unlike what is found in the lower part of the ventricle, where the dorsal wall or roof is formed merely by a prolongation of the epithelium which lines the floor and sides, in this upper part of the ventricle the roof has become developed into a large and complicated organ termed the cerebellum, which consists of a smaller central part, and two large lateral hemispheres. These are united around the ventral or anterior aspect of the cavity by a strongly marked bundle of fibres which issues on either side from the hemisphere as its so-called middle peduncle, and encircles and partly blends with what is practically a continuation upwards of the medulla oblongata, the whole forming a well-marked projection and thickening of the ventral wall of the fourth ventricle, known as the *pons Varolii.* Two other pairs of peduncles issue from the lateral hemispheres of the cerebellum, the inferior one passing downwards to the medulla, as the restiform body, the other or superior pair of peduncles being directed upwards and forwards towards the cerebrum.

THE PONS VAROLII.

The **pons Varolii** or *tuber annulare* forms a prominence marked by transverse fibres above and in front of the medulla oblongata, and between the lateral hemispheres of the cerebellum (fig. 271). Its ventral surface and upper and lower margins are arched, the superior much more so than the inferior; and at the sides its transverse fibres are gathered together into a compact mass, which passes into the cerebellum, and is named the *middle crus or peduncle of the cerebellum.* Along the middle of its ventral surface the pons has a shallow groove along which the basilar artery runs, and it is perforated by small branches of the artery. The groove is in some measure due to the circumstance that the pyramids of the medulla in being continued up through the pons with a slightly divergent course produce a prominence on either side of the middle line, covered however by the superficial transverse fibres.

The pons consists ventrally of transverse or commissural fibres, between which the longitudinal fibres prolonged upwards from the medulla oblongata pass; together with a large intermixture of grey matter. The superficial fibres on the ventral surface (fig. 272, po^2) are transverse in their general direction, but while the middle fibres pass directly across, the lower set ascend slightly, and the superior fibres (fig. 271, i), which are the most curved, descend obliquely to reach the crus cerebelli on each side; some of the upper fibres cross obliquely the middle and lower

ones, so as to conceal them at the sides. When the superficial transverse fibres are removed, the prolonged fibres of the anterior pyramids come into view; these, as they ascend through the pons, are separated into smaller bundles (figs. 272, 273, 274, *py*), intersected by other transverse white fibres, which, with those upon the surface, are all continued into the middle peduncle of the cerebellum.

Fig. 271.

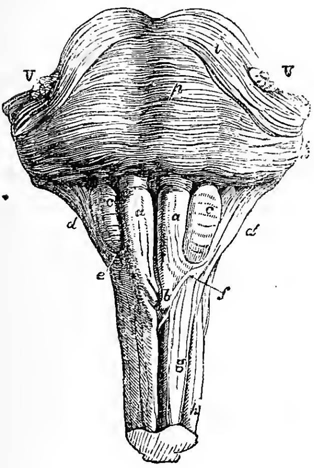


Fig. 271.—View of the anterior surface of the pons Varolii and medulla oblongata, with a small part of the spinal cord attached

a, a, pyramids; *b,* their decussation; *c, c,* olives; *d, d,* restiform bodies; *e,* external arciform fibres, curving round the lower end of the olive; *f,* fibres described by Solly as passing from the anterior column of the cord to the cerebellum; *g,* anterior column of the spinal cord; *h,* lateral column; *p,* pons Varolii; *i,* its upper fibres; v, v, roots of the fifth pair of nerves.

At the lower part of the pons, behind the fibres from the anterior pyramids, is a special set of transverse fibres (fig. 264, *p''*, fig. 272, *t*), named the *trapezium*—so called because in most of the lower animals, in which the more ventrally situated fibres of the pons are not developed and the pyramids are small, these transverse fibres partially appear on the surface between the pyramid-bundles in an area of a somewhat four-sided shape. Laterally they curve round a collection of grey matter behind them, called the superior olivary nucleus (fig. 272, *o.s.*), and probably many of them are connected with its cells. They then course outwards, across the bundles of the facial nerve-roots (*VII*), and in front of the upward prolongation of the substantia gelatinosa of the tubercle of Rolando and the bundles of fibres belonging to the ascending root of the fifth nerve (*a.V*), to join the middle peduncle of the cerebellum.

Between the bundles of fibres of this ventral portion of the pons grey matter with small multipolar nerve-cells is everywhere found (*nuclei pontis*). It is probable that many of the transverse fibres are connected with these cells, and it may be that a cell is connected at one part with a transverse or commissural fibre, and at another sends a process to reinforce the longitudinal fibres of the pyramidal tract ascending through the pons; but the same fibres do not appear to turn upwards, for the transverse fibres are smaller than the longitudinal. The interspersed grey matter seems to correspond to that which is found between the arcuate fibres of the medulla.

The posterior or dorsal portion of the pons is chiefly constituted by a continuation upwards of the formatio reticularis and of the grey matter of the medulla oblongata. As in the latter, there exists here also a median septum or raphe, which is similar in structure to that of the medulla. It does not extend through the ventral half, being obliterated, or nearly so, by the great development of the transverse or commissural fibres, except near the upper and lower borders where the superficial transverse

fibres of the pons turn in at the middle line; and especially at the upper border where bundles of the same fibres encircle the crura cerebri as they emerge from the pons.

In the reticular formation, in addition to the scattered and reticularly arranged grey matter with nerve-cells everywhere met with, there are

Fig. 272.

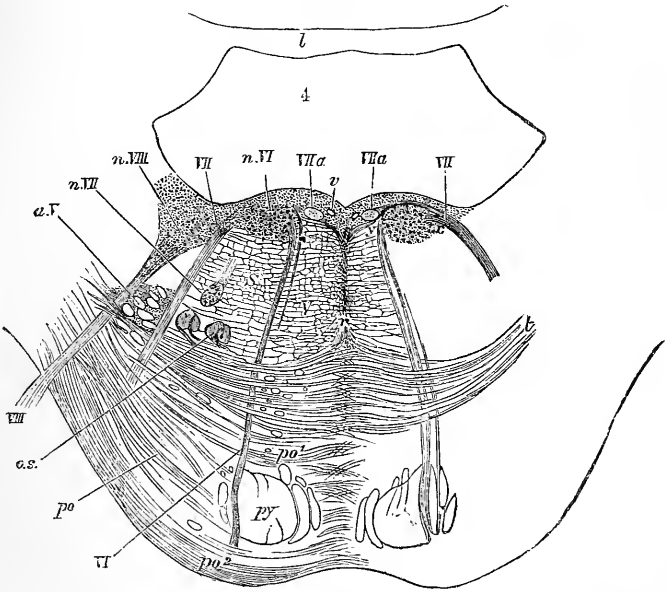


Fig. 272.—Section across the pons at about the middle of the fourth ventricle (after Stilling and Schwalbe). $\frac{3}{1}$

py, pyramid-bundles continued up from the medulla; *po*, transverse fibres of the pons passing from the middle crus of the cerebellum, before (po^2) and behind (po') the chief pyramid bundles; *t*, deeper fibres of the same set, constituting the trapezium; the grey matter between the transverse fibres is not represented either in this or in the following figures; *r*, raphe; *o.s.*, superior olivary nucleus; *a. V*, bundles of the ascending root of the fifth nerve, enclosed by a prolongation of the grey substance of Rolando; *VI*, the sixth nerve; *n.VI*, its nucleus; *VII*, the facial nerve; *VIIa*, intermediate portion of the same nerve; *n. VII*, its nucleus; *VIII*, superior root of the auditory nerve; *n. VIII*, part of its outer or superior nucleus; *v*, section of a vein.

one or two more important collections which lie embedded in this formation and from which nerve-fibres arise. One of these is the superior olivary nucleus, another is the nucleus of the seventh or facial nerve, and others give origin to portions of the fifth nerve.

The **superior olivary nucleus** (fig. 272, *o.s.*) is a collection of small nerve-cells, which lies behind the outer part of the trapezium, in what would correspond (as indicated by the passage outwards of the roots of the sixth and seventh nerves) to a prolongation of the lateral area of the medulla. In man it is very much smaller than the inferior olivary nucleus, to which it does not present much resemblance. In some animals, however, it is larger, and has a distinctly sinuous outline. From it, as above mentioned, some of the fibres of the trapezium arise.

The **nucleus of the facial nerve** (*n.VII*) lies in the reticular formation just dorsal to the superior olivary nucleus, and at some depth, therefore, below the floor of the fourth ventricle. It begins to be visible in sections immediately above the medulla oblongata, and extends three or four millimeters upwards.

The **motor nucleus of the fifth nerve** (Lockhart Clarke, fig. 273, *nV'*) comes to view above that of the facial, but it is less deeply situated, lying a little below the lateral angle of the fourth ventricle. Both it and that of the facial contain large nerve-cells.

Fig. 273.

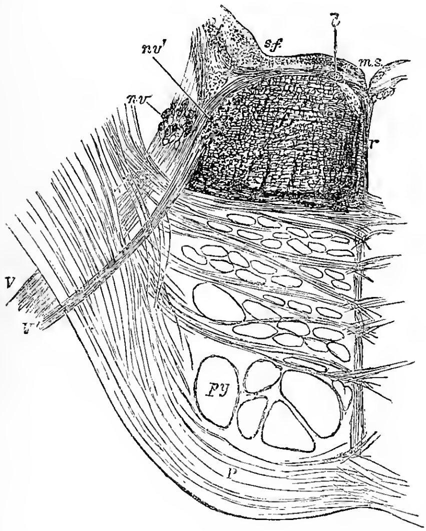


Fig. 273. — Oblique transverse section of the pons along the line of exit traversed by the fifth nerve (E.A.S.). $\frac{3}{1}$

The section passes through the lower part of the motor nucleus (*n'V*) from which a bundle of fibres of the motor root is seen passing; a part of the upper sensory nucleus (*n V*) is also shown in the section in the form of a number of small isolated portions of grey matter. Amongst these are a few bundles of the ascending root cut across, but most of these have already become diverted outwards to join and assist in forming the issuing part of the main or sensory root, *V*; *ar*, arcuate fibres near the fourth ventricle, which come partly from the raphe, partly from a small longitudinal bundle of fibres (*l*) near the median sulcus (*m.s.*), and pass outwards to join the root of the fifth nerve; *f.r.*, formatio reticularis; *r.*, raphe; *s.f.*, substantia ferruginea.

The **upper sensory nucleus of the fifth nerve** (*n. V*) lies on the outer side of the motor root. The cells are small and arranged in clusters separated by the fasciculi of origin of the nerve-root. This nucleus extends somewhat farther, both above and below, than the motor nucleus.

The rest of the grey matter of the pons lies near the dorsal surface and appears in the floor of the upper part of the fourth ventricle. Besides scattered nerve-cells, others are collected at certain parts into definite groups or nuclei from which some of the remaining cranial nerves take origin. Like the similarly placed nuclei in the medulla oblongata, these also do not lie close to the epithelium which covers the surface, but are separated from it by a layer of gelatinous substance (neuroglia) free from nerve-cells, termed the *ependyma* of the ventricle.

The **inner** or **principal nucleus of the auditory nerve** (fig. 269, *n.VIII p.*), which lies under the tuberculum acusticum, is prolonged upwards underneath the striæ acusticæ into the pons. It is widest at about the junction of the medulla and pons, where it extends almost to the middle line; further up it rapidly narrows and becomes shifted towards the lateral boundary of the ventricle as the nucleus of the

sixth nerve makes its appearance between it and the median sulcus. Its cells are small, and it is much broken up by the passage through it of fine transverse nerve-fibres.

The **outer** or **superior nucleus of the auditory nerve** (nucleus of Deiters, Laura) (fig. 272, *n.VIII*), is characterized by the large size of its cells, and lies immediately on the outer side of the main nucleus. It does not begin to be visible so far down as this, but is continued as far upwards, rather increasing in size superiorly, whereas the main nucleus

Fig. 274.

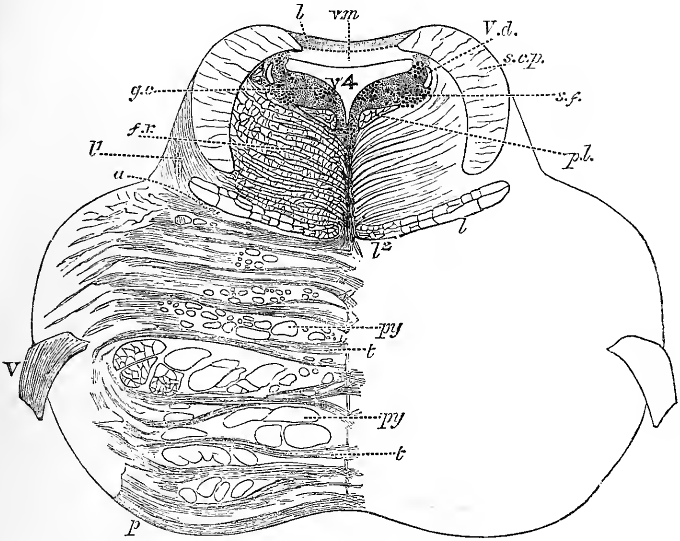


Fig. 274.—Transverse section through the upper part of the pons (Schwalbe, after Stilling). Rather more than twice the natural size.*

p, transverse fibres of the pons; *py*, *py*, bundles of the pyramids; *a*, boundary line between the tegmental part of the pons and its ventral part; *l'*, oblique fibres of the fillet, passing towards *l*, l^2, longitudinal fibres of the fillet; *f.r.*, formatio reticularis; *p.l.*, posterior longitudinal bundle; *s.c.p.*, superior cerebellar peduncle; *v.m.*, superior medullary velum; *l*, grey matter of the lingula; *v.* 4, fourth ventricle; in the grey matter which bounds it laterally are seen, *V.d.*, the descending root of the fifth nerve, with its nucleus; *s.f.*, substantia ferruginea; *g.c.*, group of cells continuous with the nucleus of the aqueduct.

diminishes. It is much broken up by longitudinal fibres. The connection of this nucleus with the auditory nerve is called in question by Laura.

The **accessory nucleus of the auditory nerve** is represented in the upper part of the medulla by a collection of nerve-cells lying in the angle between the restiform body and the two portions of the posterior root of

* The details of this and of several of the preceding figures are filled in under a somewhat higher magnifying power than that used for tracing the outlines.

the nerve (fig. 269, *n.VIII.ac*). But the chief part of the nucleus is placed higher up in the region of the pons on the outer side of the anterior root. It is remarkable for the fact that its cells, which are small and rounded but multipolar, are enclosed like those of the spinal ganglia each in a nucleated capsule.

The **nucleus of the sixth nerve** (common nucleus of the sixth and seventh of some authors) consists of a tract or column of large multipolar cells lying on either side of the median sulcus (fig. 272, *n.VI*). It corresponds to the part of the fasciculus teres which lies in front of the striæ acusticæ on the floor of the fourth ventricle. It has a close relation to the root of the facial; which runs along its mesial side (*VII.a*), curves round it eventually, and appears to receive some fibres from it, but it is somewhat doubtful if this is really the case (Gowers). Its cells are smaller than those of the facial nucleus.

Upper portion of the fourth ventricle.—The floor or anterior boundary of the upper portion of the fourth ventricle, close to which the above nuclei are for the most part situated, is marked in the middle of each lateral half by a distinct somewhat angular depression in a line with

Fig. 275.

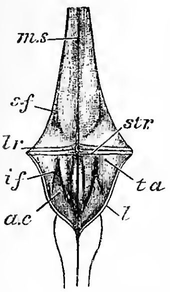


Fig. 275.—Anterior boundary (floor) of the fourth ventricle (E.A.S.). natural size.

m.s., median sulcus; *str.*, striæ acusticæ, marking the limit between the upper part of the ventricle and the lower or medullary part, calamus scriptorius; *l.r.*, lateral recess; *i.f.*, inferior (posterior) fovea; *a.c.*, ala cinerea; *t.a.*, acoustic tubercle; *s.f.*, superior (anterior) fovea, close to the lateral margin of the anterior part of the ventrtcle.

the inferior fovea, from which it is separated by the eminence over which the striæ acusticæ pass. This depression is termed the *superior fovea* (*s.f*). Between it and the median sulcus is the prolongation of the fasciculus or eminentia teres, which is prominent opposite the fovea but becomes gradually less so above and below. Extending from the anterior fovea to the upper end of the ventricle, where this narrows to the Sylvian aqueduct, is a shallow depression distinguished in the adult by its dark grey or slaty tint, which is due to a subjacent tract of pigmented nerve-cells (*substantia ferruginea*). It is known as the *locus cœruleus*.

The lateral boundaries of this part of the ventricle are formed by the superior peduncles of the cerebellum (fig. 274, *s.c.p.*, fig. 282, 5). These pass gradually to the roof of the ventricle as they extend forwards and upwards. They are at first separated from one another by a tolerably wide interval which, however, gradually narrows near the end of the ventricle, the two crura of opposite sides there approaching one another, and their margins coming in contact. The triangular interval between the two crura is bridged over by a lamina of white matter marked across with grey streaks. This is the *superior* (anterior) *medullary velum* or *valve of Vieussens* (fig. 274, *v.m.a.* in transverse section), and, with the crura, forms the posterior boundary of the upper part of the fourth ventricle. The white substance of which it is mainly composed is marked superficially by three or four flat transverse grey laminæ, with intervening sulci, which together constitute the so-called *lingula* (fig. 263, *lng*). This is continued laterally and posteriorly into the grey cortex

of the cerebellum, while the subjacent white substance of the velum is in direct continuity with the central white matter of the cerebellum, into which a pointed tent-shaped projection of the roof of the ventricle extends (fig. 279, *V4*, in longitudinal section). This projection is bounded below by the *inferior* (posterior) *medullary velum*, which in like manner is prolonged from the white substance of the central part of the cerebellum. It is less easily displayed than the superior velum, being concealed by a part of the cerebellum, which is attached to its under or posterior surface. It will be further noticed in the description of the cerebellum.

THE CEREBELLUM.

The cerebellum or hinder brain (fig. 276) consists of two lateral *hemispheres* joined together by a median portion called, from the peculiar appearance caused by the transverse furrows or ridges upon it, the *worm* or *vermiform process.* This is seen on the under surface in the fossa between the hemispheres as a well-marked projection, named the *inferior vermiform process,* but above forms only a slight elevation, the *superior vermiform process* (fig. 277, *sv*). In birds, and in animals lower in the scale, this middle part of the cerebellum alone exists, and in mammals it is the first part to be developed ; moreover, in most mammals it forms a central lobe very distinct from the lateral portions.

Fig. 276.

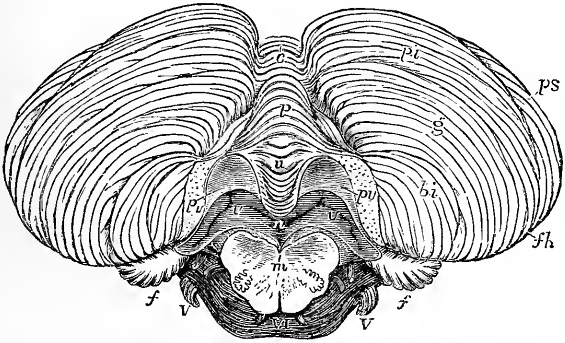


Fig. 276.—Lower surface of the cerebellum with the inferior (posterior) medullary velum (Allen Thomson after Reil and Reichert, and from nature). $\frac{2}{3}$

The medulla oblongata is cut across near the pons Varolii ; and the latter has been separated somewhat from the cerebellum in order to bring into view the posterior medullary velum. To display this better the amygdalæ have been removed.

p s, posterior superior lobe ; *f h*, horizontal fissure ; *p i*, posterior inferior lobe ; *g*, slender lobe ; *b i*, biventral lobe ; *c* to *n*, inferior vermiform process, on which are, *c*, tuber valvulæ, *p*, pyramid, *u*, uvula, *n*, nodule (the letter is placed in the fourth ventricle) ; *f*, flocculus ; *p v*, on each side, placed on the cut surface where the amygdalæ have been removed, points by a line to the lateral part of the inferior medullary velum ; its median part is continuous with the anterior surface of the nodule ; *v*, *v*, cavity of the fourth ventricle ; the cavity extends on each side into the lateral recess ; *m*, medulla oblongata ; V, VI, roots of the fifth and sixth cranial nerves.

The hemispheres are separated behind by a deep notch. The upper vermiform process, though slightly elevated, is not marked off from the

hemispheres, so that the upper surface of the organ, which is somewhat flattened in the middle and sloping downward on each side, is uninterrupted. Below, the hemispheres are convex, and are separated by a deep fossa, named the *vallecula*, which is continuous with the notch behind, and in it the inferior vermiform process (fig. 276, *c* to *n*, fig. 278, 2, 2) lies concealed in a great measure by the surrounding parts. Into this hollow the medulla oblongata is received in front, and the falx cerebelli behind.

Fig. 277.

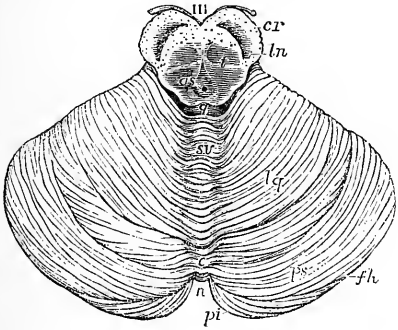


Fig. 277.—Outline of the upper surface of the cerebellum. (Allen Thomson.) ½

At the upper part of the figure the crura cerebri and parts behind them have been cut through and left in connection with the cerebellum.

III, the third pair of nerves lying upon the crura cerebri; *c r*, white matter or crust of the crura cerebri; *l n*, locus niger; *t*, tegmentum containing grey matter in the upper part of the crura; *a s*, aqueduct of Sylvius; *q*, corpora quadrigemina, the letter is placed on the central lobe of the cerebellum; *s v*, superior vermiform process; *l q* is placed on the anterior crescentic lobe, which, with the sickle-shaped posterior crescentic lobe immediately below, forms the antero-superior or quadrate lobe; *p s*, postero-superior lobe; *f h*, horizontal fissure; *p i*, postero-inferior lobe; *n*, the notch between the hemispheres.

The greatest diameter of the organ is transverse, and extends to about three and a half or four inches: its width from before backwards is about two or two and a half inches; and its greatest depth is about two inches, but it thins out towards its lateral border.

Lobes.—The cerebellum is characterised by its laminated or foliated appearance, its surface being everywhere marked by deep, closely set, transverse and somewhat curved, fissures, which extend a considerable depth into its substance, but do not all entirely encircle the organ, for many of them coalesce with one another, and some of the smaller furrows have even an oblique course between the others. Moreover, on opening the larger fissures, many folia are seen to lie concealed within them, not reaching the surface of the cerebellum. Some of these fissures are better marked than others, the most conspicuous being the *great horizontal fissure* (figs. 276, 277, *fh*), which beginning in front at the middle peduncle, extends round the outer and posterior border of each hemisphere, dipping down into the posterior notch to unite with its fellow in the middle line. This fissure divides the cerebellum into an upper and lower portion, corresponding in fact to the upper and lower surfaces, in each of which several lobes, separated by fissures for the most part deeper than the rest, are described as follows:—

1. On the upper surface of the cerebellum. The *central lobe*, (fig. 277, *q*), consists of about eight folia, immediately adjoining the anterior concave border; it is overlapped and partly concealed by the next lobe. Its central part is continued upwards on to the superior medullary velum, in the form of three or four shallow transverse laminæ, which together constitute a structure which is termed from its shape the *lingula* (fig. 263,

lng). The *antero-superior lobe*, sometimes called *quadrate*, and the *postero-superior lobe*, are placed between the central lobe and the great horizontal fissure. The quadrate lobe has a comparatively narrow part marked off from it posteriorly which is sometimes distinguished as the *posterior crescentic lobe*, the rest of the quadrate being then designated the *anterior crescentic lobe* (see description of fig. 277). These lobes and the intervening fissures, are all prolonged on to the superior vermiform process, where they are less marked than on the hemispheres. Moreover, the laminæ on that become reduced in number, the posterior superior lobe being, indeed, represented on the worm only by a single well-marked lamina, the so-called *folium cacuminis* (fig. 277, below *c*).

2. On the under surface of the cerebellum. a. On the lateral hemispheres. From behind forwards are enumerated the *posterior inferior lobe* (fig. 276, *pi*), the *slender lobe* (*g*), the *biventral lobe* (*bi*), the *amygdala* (fig. 278, 4) and the *flocculus* (fig. 276, *f*). The first three are of considerable extent; the amygdala is a small rounded lobule, projecting into the vallecula, and abutting against the inferior vermiform process, and the flocculus is a still smaller lobule which is partly concealed by the biventral lobe, between which and the middle peduncle it appears in the form of a fluted projection attached by a slender pedicle, which is traceable mesially into the edge of the inferior medullary velum (see below).

Fig. 278.

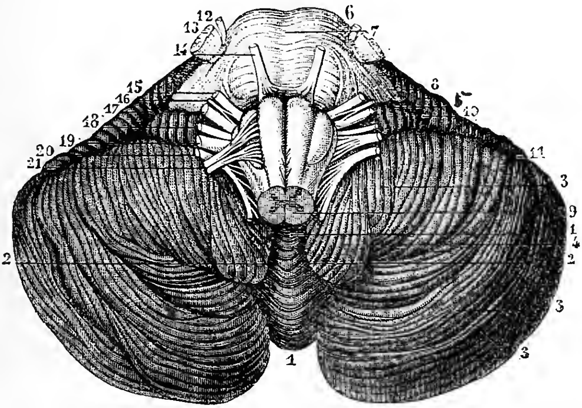


Fig. 278.—Inferior surface of the cerebellum with the pons Varolii and medulla oblongata (from Sappey after Hirschfeld and Leveillé). $\frac{2}{3}$

1, placed in the notch between the cerebellar hemispheres, is below the inferior vermiform process; 2, 2, median depression or vallecula; 3, 3, 3, the biventral, slender, and postero-inferior lobules of the hemisphere; 4, the amygdala; 5, flocculus or subpeduncular lobule; 6, pons Varolii; 7, its median groove; 8, middle peduncle of the cerebellum; 9, medulla oblongata; 10, 11, anterior part of the great horizontal fissure; 12, 13, smaller and larger roots of the fifth pair of nerves; 14, sixth pair; 15, facial nerve; 16, pars intermedia; 17, auditory nerve; 18, glosso-pharyngeal; 19, pneumogastric; 20, spinal accessory; 21, hypoglossal nerve.

b. On the inferior vermiform process. Situated most posteriorly is the *tuber valvulæ* (fig. 276, *c*), consisting of a few folia which unite the postero-inferior, and slender lobes of the two sides. In front of this is a conical projection named the *pyramid* (*p*), connected laterally with the

biventral lobes. Next is another smaller projection, the *uvula* (*u*), which is placed between the amygdalæ (removed at *p v*); these terms having been suggested by a comparison with the parts so named in the throat. The connecting ridge of grey matter between the uvula and amygdalæ on each side, but concealed from view, is named the *furrowed band*. The pointed termination of the inferior vermiform process is named the *nodule* (fig. 276, above *n*), and corresponds to the flocculi at the sides. On each side of the nodule is the lateral part of the *inferior* (posterior) *medullary velum* (*p v*), appearing as a thin white lamella of a semilunar form, which is continuous by its superior convex border with the central white substance of the worm, while the lower concave border is free, or at least continuous only with the thin epithelial covering which forms the hinder boundary (roof) of the lower part of the fourth ventricle, covering the pia mater and its choroid plexuses. The outer ends of these lateral lamellæ are attached to the flocculi, and

Fig. 279.

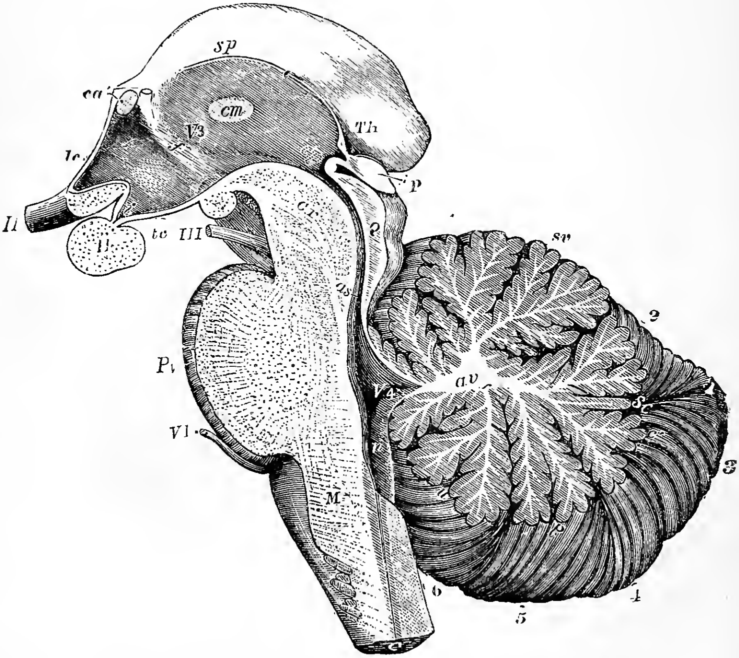


Fig. 279.—Right half of the encephalic peduncle and cerebellum as seen from the inside of a median section (Allen Thomson after Reichert).

The following letters refer to parts in connection with the medulla, pons, and cerebellum; PV, pons Varolii divided in the middle; M, medulla oblongata; *c*, central canal, divided longitudinally, with grey substance surrounding it; V4, middle of the fourth ventricle. In the cerebellum, *a v*, stem of white substance in the centre of the middle lobe of the cerebellum, ramifying into the arbor vitæ; *s v*, superior vermiform process or upper portion of the middle lobe; *s c*, single folium (folium cacuminis), which passes across between the postero-superior lobes; *c′*, the tuber valvulæ; *p*, pyramid; *u*, uvula; *n*, nodule; 1 to 2, laminæ of the antero-superior lobe; between V4 and 1 are seen the lingula and central lobe in section; 3, postero-inferior lobe; 4, lobulus gracilis; 5, biventral lobe; 6, amygdaloid lobe.

the inner ends to the anterior surface of the nodule, and to each other just below that projection. The posterior velum thus constituted is covered in and concealed by the amygdalæ, and cannot be seen until those lobules have been turned aside or removed as shown in the figure (fig. 276).

Internal structure of the cerebellum; arrangement of the grey and white matter.—The central part both of the worm and hemispheres is composed of white substance, which sends out divergent and gradually thinning layers into the interior of all the laminæ, larger and smaller, the grey substance forming everywhere a continuous covering on their surface (fig. 280). In consequence of this arrangement of the white and grey substances, sections of the cerebellum crossing the laminæ present a beautifully foliated or arborescent appearance, named *arbor vitæ* (*a v*, fig. 279). This appearance is seen in any vertical section, but it is most perfect in that which passes through the median plane, where the relative quantity of the central white matter is small. The foliations are arranged somewhat pinnately, the section of each primary lamina having those of secondary laminæ clustered round it like leaflets on a stalk.

The main branches of the white medullary substance, or groups of them, correspond with the lobules above enumerated, as indicated in the figures (figs. 279 and 280).

In the lateral hemispheres, with which the peduncles are connected, the white matter is more abundant than in the worm (fig. 280); and, if

Fig. 280.

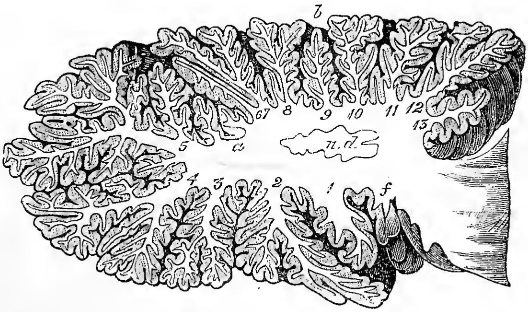


Fig. 280. — Section through one of the hemispheres of the cerebellum, to show the medullary centre and its prolongations into the primary lamellæ (Schwalbe).

n.d., dentate nucleus in the medullary centre of the hemisphere. From the latter proceed 13 primary medullary laminæ. Of these *1* belongs to the amygdala, *2* to the biventral lobule, *3* and *4* to the postero-inferior lobule, *5* to the postero-superior lobule, *6* to *12* to the antero-superior lobule, and *13* to the lateral part of the central lobule. *a*, one or two small laminæ at the bottom of the great horizontal fissure; *b*, fissure between the two parts of the quadrate lobule; *f*, stalk of the flocculus.

a section be made through either hemisphere half way between its centre and the middle of the vermiform process, it will display a nucleus of grey matter, which is named the **corpus dentatum** of the cerebellum (*n d*). This structure, very similar to that already described in the olivary body of the medulla oblongata, presents the appearance of a waved line of compact yellowish brown substance, containing white matter within. The line is interrupted at its upper inner part. In whatever direction the section is carried through the corpus dentatum, the outline has the same waved character, so that the dentate nucleus may be described as consisting of a plicated pouch or capsule of grey substance open at one

part and inclosing white matter in its interior, like the nucleus dentatus of the olivary body. The fibres which issue from it may be traced to the superior peduncles of the cerebellum and to the valve of Vieussens.

In addition to the corpus dentatum certain other portions of grey matter, which have been only more recently recognised, are found in the white centre of the cerebellum (Stilling). They are three in number on each side and are termed respectively the nucleus emboliformis, nucleus globosus, and nucleus fastigii. The *nucleus emboliformis* (fig. 281, *x*) is a small clavate mass of grey substance lying mesially to and partly covering the hilus of the dentate nucleus. On the inner side of the nucleus emboliformis, and at a somewhat lower level, is a streak of grey matter passing antero-posteriorly and ending behind in an enlarged extremity. This has been named the *nucleus globosus* (*y*). Finally, close to the middle line, where it is only separated from its fellow by a narrow septum of white matter, is a rather larger portion of grey substance, which lies in the anterior part of the white centre of the worm, and close to the upper wall of the tent-like projection in the roof of the 4th ventricle. It is termed the *nucleus fastigii* (*z*). These several portions of grey matter are not entirely isolated, but are connected here and there both with one another and with the dentate nucleus.

Fig. 281.

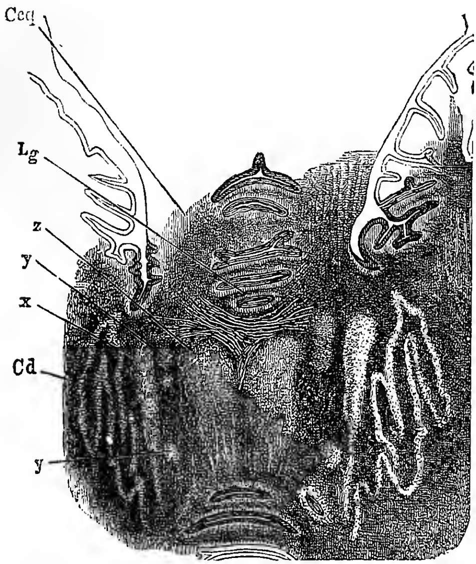


Fig. 281.—Horizontal section through the white centre of the cerebellum, showing the nuclei of grey matter (from Henle, after Stilling. $\frac{2}{1}$

The section is taken just over the roof of the fourth ventricle. The nuclei are represented lighter than the white matter in which they are embedded.

C d, corpus dentatum; x, nucleus emboliformis; y, y, nucleus globosus; z, nucleus fastigii. Above the two coalesced roof-nuclei are seen some of the fibres of the superior (anterior) decussation, and above these again the laminæ and furrows of the lingula (L g); whilst below the roof-nuclei one or two laminæ and furrows of the inferior vermiform process are included in the section. Ccq, superior cerebellar peduncle.

The **cerebellar peduncles** are constituted by white fibres which pass out from or into the white medullary substance of the hemispheres.

The *superior peduncles* (crura ad cerebrum) emerge from the mesial part of the medullary substance of the hemispheres, and run upwards and forwards towards the base of the corpora quadrigemina, under which they disappear. They are situated at first more at the side, but subsequently in the roof, of the upper part of the fourth ventricle. These peduncles are concealed by the anterior part of the cerebellum, so that to see them properly this must be divided in the middle line and turned aside. When this is done the superior crura, with the superior

(anterior) medullary velum stretched out between them, are brought to view.

The *middle peduncles* (crura ad pontem) constitute the commissure of the cerebellar hemispheres. They emerge from the lateral part of the white substance of the hemisphere, and pass forwards to become the transverse fibres of the ventral half of the pons.

The *inferior peduncles* (crura ad medullam) issue from the white matter of the lateral hemispheres, between the other two, and pass forwards immediately outside the superior peduncles to reach the lateral wall of the fourth ventricle. Here they turn sharply downwards, at a right angle, and become the restiform bodies of the medulla oblongata.

Fig. 282.

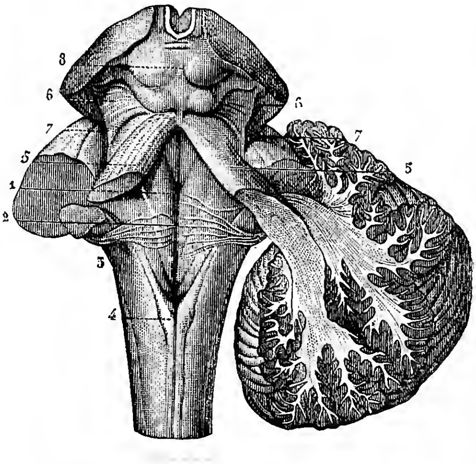


Fig. 282.—FIGURE SHOWING THE THREE PAIRS OF CEREBELLAR PEDUNCLES (from Sappey after Hirschfeld and Leveillé).

On the left side the three cerebellar peduncles have been cut short; on the right side the hemisphere has been cut obliquely to show its connection with the superior and inferior peduncles.

1, median groove of the fourth ventricle; 2, the same groove at the place where the auditory striæ emerge from it to cross the floor of the ventricle; 3, inferior peduncle or restiform body; 4, funiculus gracilis; 5, superior peduncle; on the right side the dissection shows the superior and inferior peduncles crossing each other as they pass into the white centre of the cerebellum; 6, fillet at the side of the crura cerebri; 7, lateral grooves of the crura cerebri; 8, corpora quadrigemina.

MINUTE STRUCTURE OF THE CEREBELLUM.

The **cortical grey substance** is composed of two distinct layers, viz. :—an outer clear grey layer, and an inner greyish-red "granule" layer. At the junction of the two is an incomplete layer of large cells, termed the corpuscles of Purkinje. Outside all is the pia mater, from which vascular processes extend inwards into the nervous substance.

The *outer layer* (fig. 283, *b*) consists of a delicate matrix, apparently of the nature of neuroglia, containing cells and fibres. Most of the fibres have a direction at right angles to the surface; the greater number of them are the processes of the large nerve-cells which lie between the two layers. Others are fine tapering fibres, analogous to the sustentacular fibres of the retina, and abutting by a broad base against the inner surface of the pia-mater. The cells of this outer layer are granule-like bodies, some very small, and belonging probably to the matrix, others somewhat larger and probably nervous, with processes extending from one or more sides. Some of the corpuscles are connected with the processes of the large cells of Purkinje (see fig. 284). The inner part of this layer, contiguous

with the corpuscles of Purkinje, contains nerve-fibres running parallel to the surface.

The *inner* or *granule layer* (fig. 283, *d*), next the medullary centre, consists of granule-like corpuscles embedded as close groups in a gelatinous matrix, which contains also a plexus of fine nerve-fibres. The

Fig. 283.

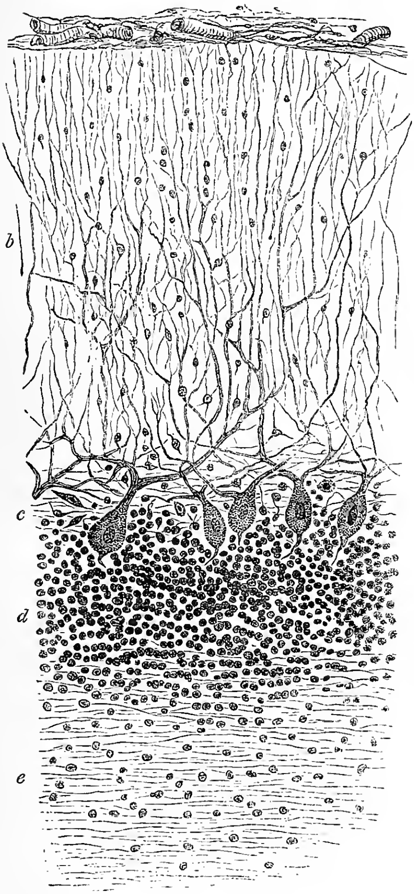


Fig. 284.

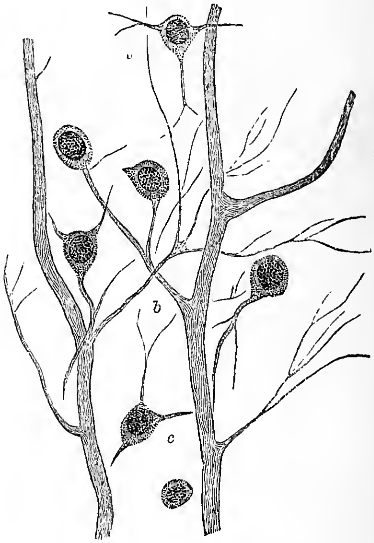


Fig. 284.—Processes of the corpuscles of Purkinje, connected, by their finer branches, with corpuscles of the outer layer of the cerebellar cortex (Sankey). Highly magnified.

a, *a*, processes of the corpuscles of Purkinje; *b*, a branch from one of them, which is connected with two of the corpuscles of the outer layer *c*, *c*, scattered branched corpuscles of this layer.

Fig. 283.—Structure of Cortex of cerebellum (Sankey).

a, pia mater; *b*, external layer; *c*, layer of corpuscles of Purkinje; *d*, inner or granule layer; *e*, medullary centre.

corpuscles vary in size from $\frac{1}{4000}$th to $\frac{1}{2500}$th of an inch, the larger being less densely scattered around the corpuscles of Purkinje. Some are round, others angular. Each cell is formed of a nucleus with a thin protoplasmic envelope, the processes from which are supposed to be connected with the plexiform nerve-fibres among which the cells lie.

The *cells of Purkinje* (fig. 283, *c*) lie between the outer and inner

layers of the grey cortex. They are more closely set at the margins of the laminæ than elsewhere. Some are irregular in form, but most are flask-shaped, their long axis being at right angles to the surface. The diameter of the larger cells is $\frac{1}{800}$th to $\frac{1}{1000}$th of an inch. Processes extend from them into both the outer and inner layers: the outer process being much the larger. It usually divides close to the cell, and its branches, either at once or after a short horizontal course, pass towards the surface, dividing repeatedly. Some are connected with the corpuscles of the outer layer (fig. 284), but most can be traced nearly to the outer surface, and are there lost. The inner process is fine, undivided, and passes into the granule layer, where it is continuous with the axis-cylinder of a nerve-fibre.

The **medullary or white centre** of each lamina, consists of nerve-fibres arranged in parallel or interlacing bundles, which pass from the central white matter of the worm or of the hemispheres, and appear to turn obliquely into the cortical grey substance. They disappear in the granule layer, and are believed to be continuous with the axis-cylinder processes of the corpuscles of Purkinje, but some are of opinion that they arise, in part at least, by the union of the fine fibres of a plexus in the outer layer.

The structure of the *corpus dentatum* resembles that of the olivary body. Stellate cells $\frac{1}{1500}$th to $\frac{1}{2500}$th inch in size, lie in grey matter which is traversed by bundles of nerve fibres, passing in various directions but chiefly from without inwards.

The *nucleus emboliformis* agrees closely in structure with the nucleus dentatus, to which it seems to bear the same relation as do the accessory olivary nuclei to the chief olivary nucleus. The *nucleus fastigii* and *nucleus globosus* differ somewhat in structure from the dentate nucleus, and chiefly in the much larger size of their cells, which, according to Meynert, are very similar to those of the so-called outer auditory nucleus or nucleus of Deiters in the pons (see p. 303).

Course of the fibres in the central white substance of the cerebellum.—Tracing the fibres of the cerebellar peduncles into the white centre of the organ, it is found that their general arrangement and distribution is as follows :—Those of the *middle peduncles* coming from the pons Varolii enter the lateral part of the white matter in two main bundles. One of these, composed of the superior transverse fibres of the pons which pass obliquely downwards over the others, radiates into the lateral and ventral parts of the medullary centre of the hemispheres (fig. 285, *m*″). The other bundle, which is formed of the lower transverse fibres of the pons, is joined at its passage into the white centre by the *restiform body* or *inferior peduncle* (fig. 285, *n*), and the fibres of both, blending in their further progress, turn upwards and radiate into the upper parts of the medullary centre of the hemispheres, and into the upper part of the worm. Those which pass into the worm curve over the corpus dentatum, and are termed by Stilling the semicircular fibres. A small part of the fibres of the restiform body is said by Stilling to enter the corpus dentatum. The *superior peduncle* passes almost entirely into the interior of the dentate nucleus, but some fibres curve round the outer side of this without passing into it, while some of the mesial fibres are traceable directly into the white substance of the worm. Probably many of the fibres of these peduncles which enter the dentate nucleus are connected with its cells, but others pass

in bundles through the grey lamina which composes it, without being thus connected. Their further course is not known, for they become lost in a feltwork of large fibres which encapsules the nucleus, but they probably go eventually to the superficial grey matter of the laminæ.

Fig. 285.

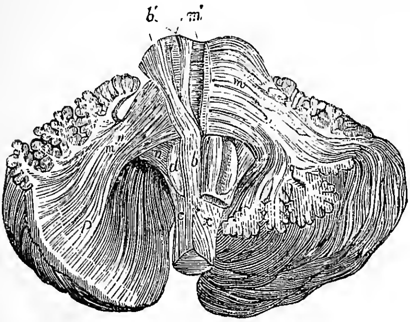


Fig. 285.—View of a dissection of the fibres of the pons Varolii and cerebellum (from Arnold). $\frac{3}{5}$

b, the pyramid; *b'*, its fibres traced upwards through the pons Varolii; *c*, lateral column; *d*, olive; *m*, superficial transverse fibres of the pons on its left side; *m'*, the deeper transverse fibres of the right side; *m''*, the prolongation of the transverse fibres of the pons as the middle peduncle of the cerebellum; *p*, *q*, their continuation into the laminæ and folia of the cerebellum; *n*, inferior peduncle; *x*, the decussating part of the left lateral column crossing to the right pyramid.

From the anterior medullary velum longitudinal fibres can be traced passing into the white centre of the worm, and blending with the semicircular fibres above mentioned.

Commissural fibres in the white matter of the cerebellum.—Two chief sets of *decussating commissural fibres* are described by Stilling in the middle line of the cerebellum; one at the anterior part of the worm at the base of the central lobule (fig. 281); the other at the posterior part. In addition to these crossing fibres, which connect the two halves of the white centre, other *collateral fibres* connect one lamina with another, passing in the white substance of the laminæ across the general direction of its fibres, and arching round the fissures between the laminæ.

The parts of the brain next to be described are entirely concealed by the cerebral hemispheres. They comprise the crura cerebri and corpora quadrigemina, the optic thalami with the middle commissure, and the pineal body, in addition to the following structures which are seen when the brain is removed from the skull and its under surface or base is examined, viz.:—the posterior perforated space, the corpora albicantia, the tuber cinereum with the infundibulum and pituitary body, the optic tracts and chiasma, and the lamina cinerea. Of these the corpora quadrigemina and crura cerebri are found in connection with the aqueduct of Sylvius, and belong to the mesencephalon, while the optic thalami and the other structures above enumerated occur in connection with the third ventricle, and belong to the thalamencephalon.

THE SYLVIAN AQUEDUCT AND PARTS IN CONNECTION WITH IT; MESENCEPHALON.

The **aqueduct of Sylvius** (iter a tertio ad quartum ventriculum) is a narrow passage into which the upper end of the fourth ventricle

gradually narrows, and which in front expands abruptly into the third ventricle. It is rather more than half an inch long. In shape it varies in different parts, being T-shaped in section below (near the fourth ventricle) triangular above (near the third), and in the intermediate part of an elongated oval form, but somewhat shield-shaped in the region of the anterior corpora quadrigemina. It is lined by ciliated columnar epithelium, outside which is a thick layer of grey matter, continuous with that of the fourth ventricle. Outside this *grey matter of the aqueduct,* the lateral and ventral parts (basal part) of the mesencephalon are composed of the thick masses of the *crura cerebri,* whilst the roof or posterior wall is formed by the *lamina quadrigemina,* so called from bearing the four mamillated tubercles known as the corpora quadrigemina.

The **grey matter of the aqueduct** is a layer of some thickness (2 to 3 millimeters) which surrounds the aqueduct, and is prolonged from the grey matter of the fourth ventricle. It is characterised by the large number of vessels which are distributed in it. It contains, scattered through its substance, nerve-cells of varying size, the largest being prolonged forwards from the locus cœruleus of the fourth ventricle; the cells are very numerous and small at the dorsal side of the aqueduct. In addition to these scattered cells the grey matter of the aqueduct contains certain more defined groups or columns of cells which are connected with the roots of the third, fourth, and fifth cranial nerves.

The **nucleus of the third and fourth nerves** extends on either side along almost the whole length of the ventral part of the aqueduct, close to the middle line, the nuclei of the two sides being only separated from one another by the raphé; superiorly they even meet across this. The cells of this nucleus are very large and irregular in shape.

The **upper nucleus of the fifth nerve** consists of a comparatively small number of large globose cells, which lie at the extreme lateral margin of the grey matter of the aqueduct close to the bundles of the descending root of the fifth nerve, towards which their axis-cylinder processes are directed.

BASAL OR VENTRAL PART OF THE MESENCEPHALON: CRURA CEREBRI.

The **crura cerebri** (fig. 260, *P*) emerge from the upper border of the pons and diverge from one another, leaving between them the posterior perforated space and the corpora mammillaria and disappearing in the cerebral hemispheres under the optic tract. Near the point of the angle of divergence the roots of the third nerves issue in several bundles from a groove along their inner side; and this groove serves to indicate the separation between the more prominent ventral part of the peduncle (*pes s. basis s. crusta pedunculi*) and the dorsal and larger part (*tegmentum*) which is in great measure concealed from view by the pes when viewed from below and in front, only appearing as a small tract on either side of the posterior perforated space. A section into the crus cerebri shows the two parts of which it is composed to be separated from one another by a tract of dark coloured grey substance known as the *substantia nigra,* which comes to the surface on the inner side at the groove above mentioned from which the third nerve issues (sulcus oculomotorii), and on the outer side also along a grooved line—the lateral sulcus.

Of the two main parts of each peduncle the *crusta* is formed almost entirely of longitudinal bundles of fibres which are continuous with the pyramid-fibres of the medulla oblongata and pons, some others being superadded, whilst the *tegmentum* is a continuation of the formatio reticularis of those parts, with the addition of much grey matter and white fibres, amongst the latter being those of the superior

Fig. 286.

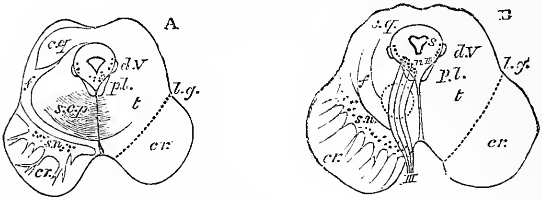


Fig. 286.—Outline of two sections across the mesencephalon. Natural size. (E. A. S. After Stilling.)

A, through the middle of the inferior corpora quadrigemina; B, through the middle of the superior corpora quadrigemina.

cr, crusta; *s n*, substantia nigra; *t*, tegmentum; *s*, Sylvian aqueduct, with its surrounding grey matter; *c.q*, grey matter of the corpora quadrigemina; *l.g*, lateral groove; *p.l*, posterior longitudinal bundle; *d. V*, descending root of the fifth nerve; *s.c.p*, superior cerebellar peduncle; *f*, fillet. The dotted circle in B indicates the situation of the tegmental nucleus.

peduncle of the cerebellum. The two ventral portions (crustæ or pedes) are entirely distinct from one another (as shown in the accompanying sections, fig. 286), and each is marked off externally from the tegmentum of the same side by the grooves just mentioned; but the two tegmenta are closely united in the middle line by a prolongation of the raphé, and extend dorsally at the sides of the aqueduct to become continuous with the bases of the corpora quadrigemina.

Crusta, pes or basis of the crus cerebri: proper cerebral peduncle. The crusta is semilunar in section, the substantia nigra projecting into it with a convex border. It is wholly made up of longitudinal white fibres which are arranged in flattened bundles, with their edges in and out, separated from one another by processes of pia mater. The main part is a direct prolongation of the pyramid-bundles of the pons and passes superiorly towards the internal capsule of the cerebral hemisphere.

Close to the substantia nigra, the bundles of white fibres are smaller and somewhat separated by projections of the grey matter extending between them. These have both a different origin and a different destination from the other fibres of the crusta; for on the one hand they are traceable from the formatio reticularis of the medulla and pons, and on the other hand they for the most part terminate in the cells of the substantia nigra, although some of them pass on to the lenticular nucleus of the corpus striatum (Meynert). They have received the name of *stratum intermedium*. Further, according to Meynert, the outer or lateral bundles of the crusta have also an origin and destination different from the main tract. He states that they are traceable from the posterior columns of the spinal cord and lower part of the medulla, crossing over to the opposite side just above the decussation of the lateral pyramidal tract (upper pyramidal decussation, fig. 267, *s. p. d.*) and then passing up with this through the medulla, pons, and crura

cerebri to spread out directly in the posterior lobes of the cerebrum without becoming connected with any of the ganglionic masses at the base of the hemispheres. Lastly the mesially situated bundles of the crusta appear also to be distinct from the pyramidal tract proper (Flechsig), being developed at a somewhat later period. Thus there have been traced at least four different sets of fibres in the crusta, and a fifth set may perhaps be added to include fibres derived originally from the cerebellum and joining the pyramidal tract in its passage through the pons, such fibres being probably scattered amongst the fibres of the other tracts.

It is remarkable that whereas in the lower part of its course (spinal cord and medulla) the fibres of the pyramidal tract acquire a medullary sheath later than the other fibres of the white columns, in the upper part (crus cerebri and cerebrum) it is acquired earlier than in the other fibres.

The **substantia nigra** is a mass of grey matter which is characterised by the presence of a number of very darkly pigmented irregular nerve-cells, which give the substance on which they are scattered the appearance from which it derives its name. It forms a layer which separates the basis or crusta from the tegmentum. It is thicker near the mesial border of the peduncle than laterally, where the tract of the fillet may be but incompletely separated from the longitudinal bundles of the crusta. It commences at the upper margin of the pons, and can be traced as far forwards as the posterior border of the corpora albicantia. At the origin of the third nerve it is traversed in its mesial part by the fibres of the nerve-root. The grey matter of the substantia nigra projects here and there between the adjacent bundles of the crusta; one considerable projection in particular in the posterior part of the mesencephalon serving to mark off the mesial portion of the crusta from the rest.

The cells in this projection are much smaller, and relatively more numerous than in the rest of the substantia nigra.

The **tegmentum**, like the formatio reticularis of the medulla and pons, of which it is the prolongation upwards, is composed of small longitudinal bundles of white fibres, separated by transversely coursing or arched fibres, together with a considerable amount of grey matter containing scattered nerve-cells. Many of the longitudinal fibres are probably continued from the anterior columns of the cord, and above they may be traced into the optic thalami.

In addition to these diffused bundles of longitudinal fibres there are some others which are collected into more defined tracts. One such tract constitutes the *posterior longitudinal bundle*, which is seen in all sections of this part of the brain as a pyriform area of transversely cut fibres which lies on each side of the middle line between the grey matter underlying the aqueduct, and the formatio reticularis (fig. 286, *p.l*). The fibres which constitute this bundle below have already been noticed (see p. 298 and fig. 274); traced upwards the bundle disappears near the posterior commissure, either by its fibres becoming dispersed in the rest of the formatio reticularis, or by their having become united with the nerve-nuclei (3rd and 4th) in the mesencephalon.

Another tract of longitudinal and decussating fibres is derived from the superior peduncle of the cerebellum, which we have already traced as it passes forwards over the anterior end of the fourth ventricle. Reaching the sides of the aqueduct as a well-marked bundle, of semilunar shape in section (fig. 274, *s.c.p*), it gradually takes a lower position as it is traced upwards in the mesencephalon, and its fibres soon begin to pass across the raphé, decussating with those of the other side (fig. 286, A), the decussation extending as far forwards as the superior

pair of corpora quadrigemina. Having thus entirely crossed to the opposite side the tract in question pursues its course longitudinally upwards, enclosing in its passage a tract of grey matter with numerous large pigmented cells, known as the *nucleus of the tegmentum* or *red nucleus* (fig. 286, B, and fig. 288), probably receiving an accession of fibres from these cells. Above, the tract passes into the ventral part of the optic thalamus.

Lastly, in sections across the upper part of the pons a considerable flattened bundle of longitudinal fibres (tract of the fillet, fig. 274, *l*) begins to make its appearance at the ventral border of the formatio reticularis, and is traceable upwards into the same part of the tegmentum. Soon, however, the longitudinal fibres of this tract are seen to pass obliquely outwards and emerge at the side of the crus cerebri, curving obliquely over the outer side of the prolongation of the cerebellar peduncle (fig. 286, A, *f*), and tending for the most part towards the inferior corpora quadrigemina. They are seen on the surface as a tract of obliquely curved fibres known as the *fillet* (lemniscus) occupying a triangular area at the side of the tegmentum (fig. 287, *f*). They are reinforced by fibres from the anterior medullary velum which also curve round the superior cerebellar peduncle. The fillet is covered externally by a thin layer of grey matter containing nerve-cells.

All the fibres of the tract of the fillet do not, however, take the course above indicated. Those nearest the middle line (inner portion, fig. 274, l^2) are said by Meynert to pass upwards in the stratum intermedium of the crusta. Those next in order (middle portion) according to Forel are for the most part continued upwards in the formatio reticularis of the tegmentum, but (with the exception of a small part which runs to the corpus albicans) become lost amongst its longitudinal bundles and are no longer traceable as a distinct tract. Some of the lateral fibres of this middle portion, however, pass to the upper corpora quadrigemina (fig. 286, B, *f*). It is especially the lateral portion of the tract of the fillet which passes to the side and enters the lower corpora quadrigemina. This is sometimes distinguished as the *lower fillet* from the tract which enters the upper quadrigeminal bodies (*upper fillet*). Traced downwards the fibres of the fillet pass into the posterior part of the lateral column of the medulla oblongata, and also, according to Roller, into the anterior column.

The *arcuate fibres* of the formatio reticularis of the tegmentum include besides the decussating fibres of the cerebellar peduncles, and the curved fibres of the fillet, others the origin and destination of which are but imperfectly understood. Some are said to be derived from the cells of the nucleus of the tegmentum before mentioned, and others from certain large spheroidal nerve-cells in the lateral part of the grey matter of the aqueduct (upper nucleus of the 5th nerve).

Dorsal part of the mesencephalon: corpora quadrigemina. As before stated the Sylvian aqueduct is covered on its dorsal aspect by the quadrigeminal lamina, bearing the bodies of the same name. The mesial part of the lamina is marked by a comparatively wide groove, shallower inferiorly, which serves to separate the corpora quadrigemina of opposite sides (fig. 282). This grooved surface, which is raised above the level of the upper medullary velum immediately behind, is connected with the velum by a small median strand of longitudinal fibres termed the *frenulum veli* (fig. 287, *fr*). In front of the upper (anterior) pair of corpora quadrigemina the groove is interrupted by a transverse white prominence—the *posterior commissure;* but both this and the upper end of the median groove are in the natural condition concealed by the pineal body (*p*), which projects backwards and downwards from the posterior wall of the third ventricle and rests between the upper pair of quadrigeminal bodies. A well-marked narrow transverse groove which commences a short distance from the middle line and is curved round the lower border of the upper tubercle separates this from the lower tubercle of the same side

The **corpora** or **tubercula quadrigemina** are two pairs of rounded eminences which are mainly composed of grey matter, although covered

Fig. 287.

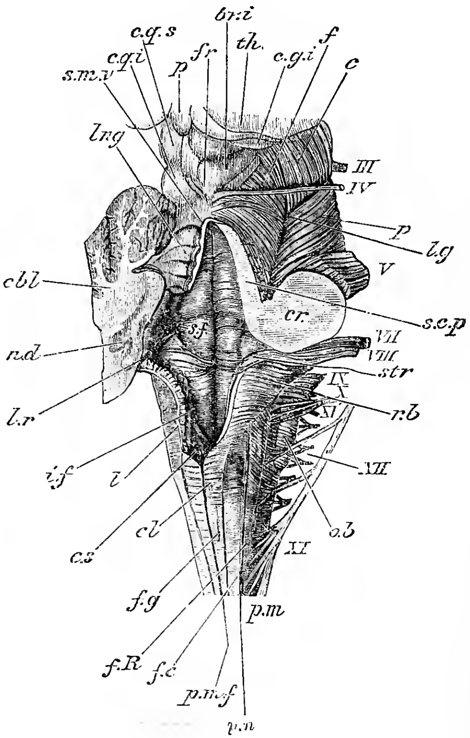


Fig. 287.—View of the medulla, pons, and mesencephalon from the right side and behind (E.A.S.)

The cerebellum, the inferior medullary velum, and the right half of the superior medullary velum, have been cut away, so as to display the fourth ventricle.

c.q.s, *c.q.i*, superior and inferior quadrigeminal bodies of the left side ; the pineal gland, *p*, is seen projecting backwards between the superior bodies, and the frænulum, *f r*, passes up from the superior medullary velum, *s.m.v*, to the interval between the posterior quadrigeminal bodies ; *th*, right thalamus opticus ; *br.i*, brachium of the inferior quadrigeminal body passing underneath the inner geniculate body, *c.g.i.* ; *f*, superficial stratum of fibres of the fillet, covering the tegmentum of the crus cerebri ; *c*, crusta of the crus cerebri, separated from the tegmentum by the lateral groove, *l.g.* ; *p*, upper part of the pons ; III., IV., etc., the corresponding cranial nerves. The rest of this figure will be found described at p. 286.

externally with a thin layer of transverse white fibres. The upper or anterior tubercles (fig. 287, *c.q.s.*) are somewhat broader and darker in colour, but slightly less prominent than the lower or posterior (*c.q.i*). Laterally the corpora quadrigemina are not bounded by a groove but each appears to be prolonged obliquely upwards and forwards into a prominent white tract, known as the *brachium* of the corresponding tubercle. The lower (posterior) brachium (fig. 287, *br.i.*) loses itself underneath an oval prominence which is seen at the side of the upper end of the crus cerebri and is termed the *inner geniculate body* (fig. 287, *c.g.i.* ; fig. 261, *i.*) ; from the opposite side of this, one of the roots of the optic tract passes. The upper (anterior) brachium passes between the same geniculate body, and the prominent posterior extremity of the optic thalamus with the external geniculate body (fig. 261, *Th*, *e*) directly into the optic tract, of one of the roots of which it may be regarded as a prolongation ; but the continuity into this is much better seen in some animals than in man.

The **lower or posterior quadrigeminal bodies** are composed almost entirely of grey substance (the so-called *nucleus* of these bodies (fig. 286A, *c.q*)) which is separated by a thin layer of the fillet from the grey matter of the aqueduct and contains numerous small and some larger nerve-cells. The nuclei are united across the middle line by a commissural

portion of grey matter which is bounded superficially and deeply by transverse white fibres derived from the fillet.

The superficial fibres are continuous laterally and in front with the fibres of the brachium of the inferior quadrigeminal body, and laterally and behind with those of the lower fillet. According to Meynert the fibres of the lower fillet on one side pass obliquely across the quadrigeminal bodies to emerge as the brachium on the other side; this continuity, however, if it really exists, is probably not direct but occurs through the medium of the nerve-cells in the grey matter.

Fig. 288.

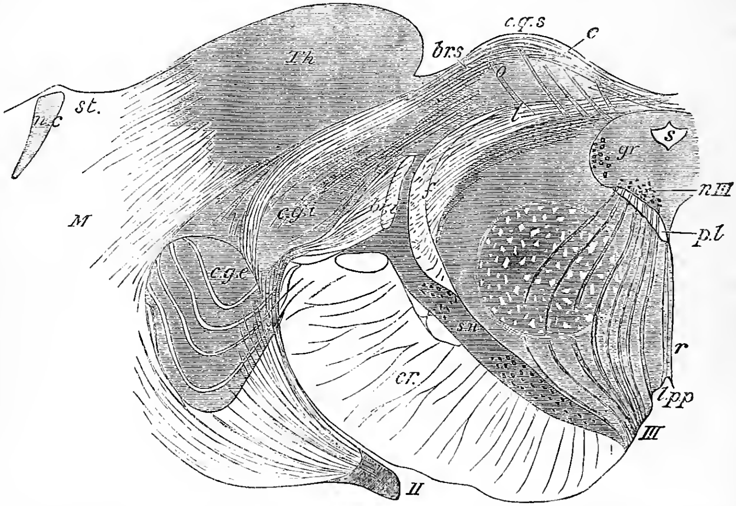


Fig. 288.—Section through the superior part of one of the superior corpora quadrigemina and the adjacent part of the optic thalamus (after Meynert).

s, aqueduct of Sylvius; *gr*, grey matter of the aqueduct; *c.q.s*, quadrigeminal eminence, consisting of: *l*, stratum lemnisci; *o*, stratum opticum; *c*, stratum cinereum: *Th*, thalamus (pulvinar); *c.g.i*, *c.g.e*, internal and external geniculate bodies; *br.s*, *br.i*, superior and inferior brachia; *f*, fillet; *p.l*, posterior longitudinal bundle; *r*, raphé; III, third nerve; *n.* III, its nucleus; *l.p.p*, posterior perforated space; *s.n*, substantia nigra; above this is the tegmentum with its nucleus, the latter being indicated by the circular area; *cr*, crusta; II, optic tract; *M*, medullary centre of the hemisphere; *n.c*, nucleus caudatus; *st*, stria terminalis.

The **upper or anterior quadrigeminal bodies** are covered, like the lower, with a thin stratum of white fibres (*stratum zonale*). Within this is a cap-like layer of grey matter (*stratum cinereum*, fig. 288, *c*), containing numerous small nerve-cells, of considerable thickness at the most prominent part of the tubercle, but thinning off towards its margins. Within this, again, is the most characteristic part of the organ. This is a layer of longitudinally coursing bundles of fine nerve-fibres (*stratum opticum*, *o*), between which lie small scattered nerve-cells embedded in grey matter, which is continuous peripherally with that of the stratum cinereum. In front the nerve-fibres pass outwards and forwards into the upper brachium (*br. s*), and along this into the optic tract. Fine fibres from the next layer pass vertically into this stratum. Lastly, between the optic-fibre layer and the grey matter around the aqueduct is a fourth well-marked layer composed of medullated fibres derived from the upper fillet (*stratum lemnisci*, *l*). This is thicker at the side, where the fillet

enters, and becomes gradually thinner near the middle line, where many of its fibres pass across, decussating with fibres from the opposite side. The gradual thinning of the stratum appears to be due to the passage of its fibres outwards into the optic-fibre layer; but some fibres (according to Tartuferi, whose comparative investigations have thrown much light upon the minute anatomy of this part) pass inwards towards the grey matter of the aqueduct.

The stratum cinereum and stratum opticum of the upper quadrigeminal body appear together to correspond to the nucleus of the lower quadrigeminal body; the stratum zonale to the superficial white layer, and the stratum lemnisci to the deeper white layer, which is also, as above mentioned, traceable to the fillet.

The connexion of the anterior quadrigeminal bodies with the optic tract and the sense of sight is far more intimate than that of the posterior. For if in a young animal the eye on the one side be extirpated, the operation is found to be followed after some time by atrophy of the anterior quadrigeminal body and of its brachium, whereas the posterior quadrigeminal body and brachium is unaltered (Gudden). Moreover in the mole the posterior quadrigeminal body is well developed, whereas the anterior is atrophied.

The **posterior commissure,** which overlies the upper end of the aqueduct and appears in the posterior wall of the third ventricle, is generally described with that cavity. It is, however, a direct continuation of the commissural fibres of the fillet above mentioned. Its fibres come from the tegmental part of the mesencephalon, and after crossing to the other side appear to pass through the thalamus and diverge into the white substance of the cerebral hemispheres. They may in part comprise commissural fibres between the two thalami. Some are connected with the pineal body.

THE THIRD VENTRICLE AND THE PARTS IN CONNECTION WITH IT: THALAMENCEPHALON.

The Sylvian aqueduct expands suddenly immediately after passing beneath the posterior commissure into a comparatively large, laterally compressed cavity, termed the **third ventricle** (figs. 289, 290). This, which is on the whole deeper in front than behind, gradually narrows at its anterior end to a conical termination which lies over the optic commissure. Below and behind this is a conical depression, leading towards the pituitary body. At the posterior extremity, immediately above the entrance of the aqueduct and separated from it by the posterior commissure, is another smaller depression extending into the stalk of the pineal gland (fig. 290, *p*), which here, as we have seen, projects backwards over the mesencephalon. The ventricle is bounded laterally by the *optic thalami* (fig. 289, *Tho*), which come almost in contact with one another in the middle line; and a little in advance of the middle of the ventricle, are actually united by a connecting band of grey matter of variable extent, termed the *middle* or *soft commissure* (*Com.*) This is sometimes double, and occasionally wanting: it is liable to be torn across in removing the brain. The lateral walls of the cavity are slightly convex, and are marked towards the anterior end by a white curved band, with its convexity forwards, which becomes more prominent as it passes upwards towards the roof. These bands are named the *anterior pillars of the fornix* (fig. 290, *f*). Immediately behind the most prominent part of each of these, between it and the anterior part of the thalamus, is an

aperture (*foramen of Monro*) leading into the ventricle of the hemisphere (lateral ventricle). All along the upper curved margin of the lateral wall, from the pillar of the fornix to the pineal gland, runs a white stria, known as the *stria pinealis*, or *tænia fornicis* (fig. 290, *sp*; fig. 289, *Tfo*). The floor of the ventricle is formed posteriorly by the *tegmenta* of the crura cerebri, and where the crura diverge from one another by the following parts, which have been already mentioned as seen at the base of the cerebrum; viz., commencing from behind, the *posterior perforated space*, the *corpora albicantia*, the *tuber cinereum* and *infundibulum*, and the *lamina cinerea*, the last of which also serves to close the ventricle in front. The roof of the cavity is limited before and behind by two commissures, named from their position, anterior and posterior. Of these the anterior belongs to the description of the cerebral hemispheres, while the posterior has already been noticed in connection with the mesencephalon.

Fig. 289.

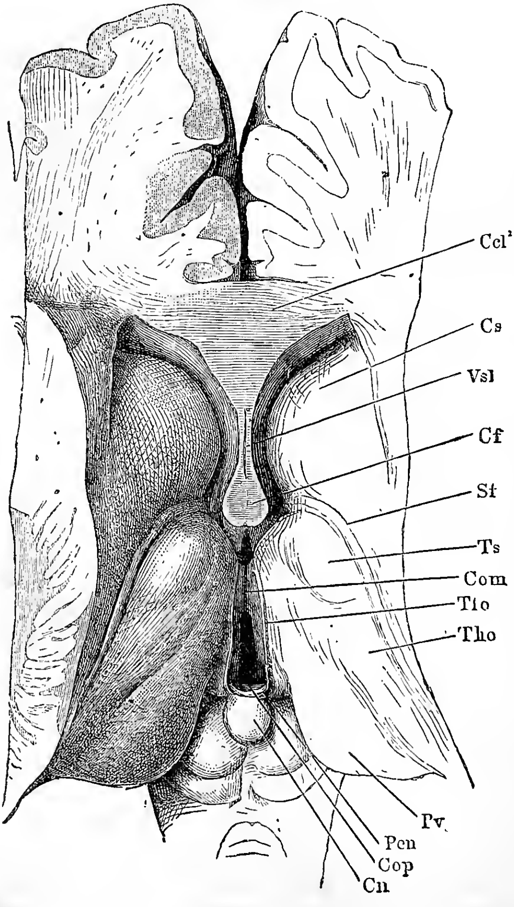


Fig. 289. — View from above of the third ventricle and a part of the lateral ventricles (Henle).

The brain has been sliced horizontally immediately below the corpus callosum, and the fornix and velum interpositum have been removed.

Tho, thalamus opticus; *Ts*, its anterior tubercle; *Pv*, pulvinar; *Com*, middle commissure stretching between the two optic thalami across the middle of the third ventricle; *Cf*, columns of the fornix; *Cn*, pineal gland projecting downwards and backwards between the superior corpora quadrigemina; *Sf*, stria terminalis; *Cs*, nucleus caudatus of the corpus striatum; *Vsl*, ventricle of the septum lucidum; *Ccl*², section of the genu of the corpus callosum; *Pen*, commencement of the pineal stria or peduncle, *Tfo*; *Cop*, posterior commissure.

The third ventricle, like the fourth, is roofed over by the epithelial lining of the central cerebro-spinal cavities. This epithelial covering is not free but covers the under surface of the median portion of an expansion of pia mater named the *velum*

interpositum, which overlies the third ventricle as well as the larger part of the optic thalami. The epithelium follows all the inequalities of two fringed vascular tracts (*choroid plexuses*) which project downward from the membrane; and, therefore, becomes torn away when the pia mater is removed. At the white stria on either side it is continuous with the epithelium covering the lateral wall.

Fig. 290.

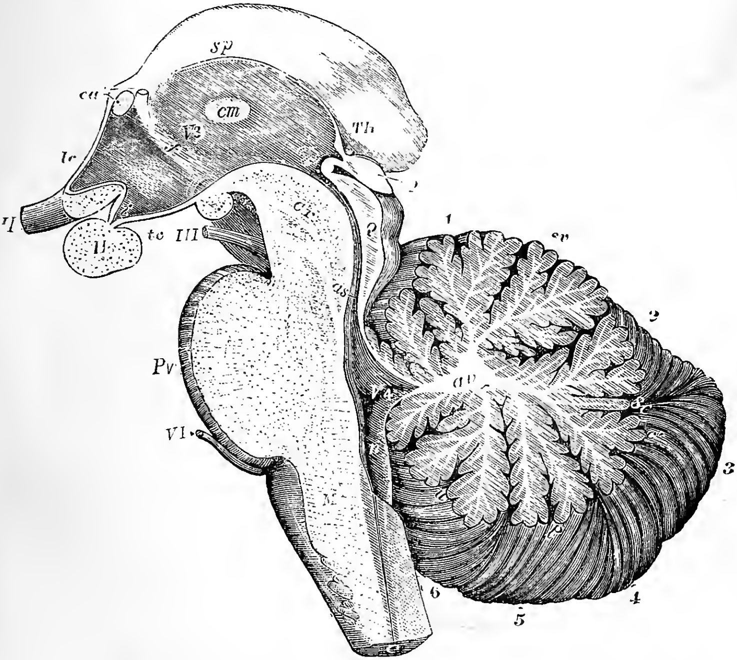


Fig. 290.—Right half of the encephalic peduncle and cerebellum as seen from the inside of a median section (Allen Thomson after Reichert).

II, right optic nerve; behind it the optic commissure divided; III, right third nerve; VI, sixth nerve; V 3, third ventricle; *Th*, back part of the thalamus opticus; *H*, section of the pituitary body; *p*, pineal gland; below its stalk is the posterior commissure; *c a*, anterior commissure divided, and behind it the divided anterior pillar of the fornix; *l c*, lamina cinerea; *i*, infundibulum (cavity); *t c*, tuber cinereum; behind it the corpus albicans; *f*, mark of the anterior pillar of the fornix descending in the wall of the third ventricle; *c m*, commissura mollis; *s p*, stria pinealis or peduncle of pineal gland; *Q*, lamina quadrigemina; *a s*, aqueduct of Sylvius near the fourth ventricle; *cr*, crus cerebri; *P V*, pons Varolii; *M*, medulla oblongata; and behind these the cerebellum.

The third ventricle is lined like the other cavities already described by ciliated epithelium, which is thin and flattened over the roof, *i.e.* lining the velum and choroid plexuses, but longer and more columnar at the bottom and sides. The floor, which is narrow, is formed, underneath the epithelium, of grey matter continuous with that of the Sylvian aqueduct, and this grey matter extends a short distance upwards on the wall of the thalamus. The central grey substance behind rests upon the still conjoined part of the tegmenta; but anteriorly, after these have diverged, it comes to the surface at the base of the brain as the posterior perforated lamina and the tuber cinereum. The lateral walls of

the ventricle have but a thin covering of neuroglia (ependyma) underneath the lining epithelium; so that the white covering of the thalami comes to view through it.

The **optic thalami** (fig. 289, *Tho*), as seen from above after the removal of the fornix and velum interpositum, are somewhat oval-shaped masses of grey substance covered superficially by a thin stratum of white fibres. The upper surface is marked by a shallow longitudinal groove, which inclines inwards as it passes forwards, and terminates a short distance from the anterior extremity of the surface. This anterior extremity is raised into a prominence termed the *anterior tubercle* (fig. 289, *Ts*), and together with the part of the upper surface which is placed outside the groove, projects into the ventricle of the corresponding cerebral hemisphere, and is covered by the lining epithelium of that cavity. This part of the upper surface is limited externally by a white band, the stria terminalis, (*Sf*) which separates it from the part of the corpus striatum which is seen in the lateral ventricle. The longitudinal groove appears to be caused by the thickened margin of the fornix, the edge of which extends over the surface of the thalamus along the line of the groove. The posterior and inner part of the upper surface behind the groove does not project into either the third or the lateral ventricle, and is not covered with epithelium. It is limited internally by a sharp edge which separates it from the median surface and which is marked by the medullary stria above-mentioned as leading to the pineal body. At the posterior and inner extremity of the thalamus, there is seen, as in front, a well-marked prominence (*posterior tubercle* or *pulvinar* (*Pv*)) which projects over and partially conceals the brachia of the corpora quadrigemina. Between this prominence and the peduncle of the pineal body (*Pen*) lies a small triangular depressed surface, separated posteriorly from the mesencephalon by a transverse groove and passing mesially into the stalk of the pineal body. This triangular surface is termed the *trigonum habenulæ*. The mesial surface of the thalamus has been already described in connection with the third ventricle. The posterior rounded surface is occupied almost entirely by the pulvinar. Below and external to this is another distinct eminence termed the *outer geniculate body*, which is placed just above the *inner geniculate body* before mentioned (p. 319), the two being separated from one another by one of the roots of the optic tract (upper brachium) (fig. 261). From this brachium and from the two geniculate bodies the optic tract originates and curves downwards and forwards around the crus cerebri.

The external and under surfaces of the thalamus are not free, but are united with other parts of the brain. The under surface is united with the tegmental part of the crus cerebri, while the external surface is covered by white substance which is formed of the fibres of the crusta, which here diverge into the substance of the hemisphere, and pass between the thalamus and the lenticular nucleus forming the so-called "internal capsule." More anteriorly the corpus albicans and the side of the tuber cinereum lie below the thalamus.

Structure.—The thalami optici are covered on their free surfaces (inner and upper), (fig. 291), by a layer of white fibres. On their outer surface, as just mentioned, is the white matter of the inner capsule (*i. c.*) formed by fibres diverging from the crusta into the hemispheres. Next to the thalamus on this side is a denser layer of white fibres, termed the outer medullary lamina. All along

this surface radiating fibres pass out of the thalamus to mingle with the fibres of the inner capsule and to pass with these to the surface of the cerebral hemispheres. Those in front pass to the frontal lobe of the hemisphere; those in the middle region to the posterior part of the frontal and to the parietal lobe, besides some to the temporo-sphenoidal; those behind to the temporo-sphenoidal and occipital lobes. Continuous with these radiating fibres are others passing to the optic tract from the pulvinar. The lower surface of the thalamus is continuous posteriorly with the prolongation of the tegmentum (subthalamic tegmental region), but in front this prolongation inclines to the outer side and becomes lost in a layer of grey matter which is continuous internally with the grey matter of the floor of the ventricle, and is seen at the base of the brain as the anterior perforated lamina. Anteriorly the under surface of the thalamus is prolonged into a tract of fibres which curves downwards and outwards towards the white substance of the hemisphere forming the so-called lower peduncle of the thalamus. Above these is another tract (*ansa lenticularis*) passing under the thalamus from the mesial part of the crusta to the lenticular nucleus of the corpus striatum, a layer of grey substance being interpolated between the two tracts. These and the grey matter between are termed collectively the *substantia innominata.*

Fig. 291.

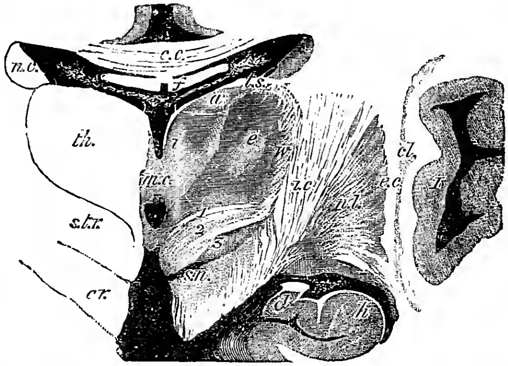


Fig. 291.—Section across the optic thalamus and corpus striatum in the region of the middle commissure (E.A.S., after a preparation by Mr. S. G. Shattock). Natural size.

th, thalamus; *a*, *e*, *i*, its anterior, external and internal nuclei respectively; *w*, its latticed layer; *m. c.*, middle commissure; above and below it is the cavity of the third ventricle; *c. c.*, corpus callosum; *f*, fornix, separated from the third ventricle and thalamus by the velum interpositum. In the middle of this are seen the two veins of Galen and the choroid plexuses of the third ventricle; and at its edges the choroid plexuses of the lateral ventricles; *t. s.*, tænia semicircularis; *cr*, forward prolongation of the crusta passing laterally into the internal capsule, *i. c.*; *s. t. r.*, subthalamic prolongation of the tegmentum, consisting of (1) the dorsal layer, (2) the zona incerta, and (3) the corpus subthalamicum; *s. n.*, substantia nigra; *n. c.*, nucleus caudatus of the corpus striatum; *n. l.*, nucleus lenticularis; *e. c.*, external capsule; *cl*, claustrum; *I*, island of Reil.

The substance of the thalamus is chiefly formed of grey matter with nerve-cells scattered in it, but their arrangement and connections with nerve-tracts have not hitherto been satisfactorily ascertained. Its grey matter is partially subdivided into two parts, the so-called inner and outer nuclei of the thalamus (Burdach), by a vertical white lamina, S-shaped in section (inner medullary lamina). The *outer nucleus* (*e*), is the larger and extends into the posterior tubercle; it is marked externally by the radiating white lines before mentioned as passing from the thalamus into the inner capsule, and these confer upon its external layer somewhat of a reticulated aspect (latticed layer). The *inner nucleus* (*i*) does not extend into the anterior tubercle, but this part of the grey substance of the thalamus is cut off from it by another septum of white matter. The anterior separated part is the *anterior nucleus* of the thalamus or *nucleus of the anterior tubercle* (*a*). It contains comparatively large nerve-cells and from its depth a number of fibres pass downwards and converge to form a well-marked bundle (bundle of Vicq-d'Azyr), which entering the corpus albicans forms within that tubercle a sharp bend, and passes upwards again in the wall of the ventricle as the anterior pillar of the fornix. The middle commissure unites

the inner nuclei across the third ventricle and is also continuous below on each side with the grey matter of the cavity. It contains transversely coursing fibres and nerve-cells.

In the *trigonum habenulæ* is a collection of nerve-cells termed by Meynert the *ganglion of the habenula*. From this a bundle of fibres is traceable downwards towards the interpeduncular region (the part between the cerebral peduncles) to another collection of nerve-cells, better marked in most animals than in man, termed the *interpeduncular ganglion* (Forel).

The *outer geniculate body*, darker in colour than the rest of the external nucleus of the thalamus to which it is attached, has a lamellated structure (fig. 288, *c.g.e.*); thin layers of white fibres derived from the optic tract alternating with thicker layers of grey matter containing large, pigmented, multipolar nerve-cells. The actual connection of the fibres with the cells has not been traced, but there is no doubt that this prominence and the neighbouring part of the thalamus are connected with the origin of the optic fibres, from the atrophy which they undergo after extirpation of the opposite eye.

The *inner geniculate body*, also continuous with the grey substance of the thalamus, lies below and mesial to the external geniculate body and receives inferiorly and on its inner side the brachium of the lower quadrigeminal body which dips underneath it. Externally and in front fibres pass out from it to join the optic tract. It is believed that these fibres are of commissural nature, and are not continued into the optic nerve, for they, as well as the inner geniculate body, remain unaffected by extirpation of the opposite eye.

Subthalamic tegmental region.—The prolongation of the tegmentum under the posterior part of the thalamus is divided by Forel into three layers, which are named respectively from above down, the stratum dorsale, the zona incerta, and the corpus subthalamicum (fig. 291, *s. t. r.*, 1, 2, 3). The latter is bounded below by a continuation of the substantia nigra, separating it from the prolongation of the crusta, the fibres of which are seen diverging at the side of the subthalamic tegmental region into the inner capsule. The *dorsal layer* consists chiefly of fine longitudinal fibres—prolonged from the posterior longitudinal bundle according to Meynert, from the fibres enclosing the tegmental nucleus (derived therefore from the superior cerebellar peduncles) according to Forel. It is continuous laterally with the latticed layer and external medullary lamina of the thalamus, into which some of its fibres pass, whilst others, coursing through the zona incerta, enter partly the inner capsule, and partly the substantia innominata, joining a tract which leads to the lenticular nucleus of the corpus striatum.

The *zona incerta* is a reticular formation prolonged from that of the mesencephalon; it passes anteriorly into the substantia innominata.

The *corpus subthalamicum* is a well-marked brown stratum of grey matter containing numerous pigmented nerve-cells. It is lens-shaped in section, and has an enclosing envelope of white substance, through which strands of fine fibres pass from the interior of the body mesially towards the posterior perforated lamina, and outwards and downwards into the crusta. This stratum is distinct only in the Primates.

The **pineal body** or **gland** (conarium) (fig. 289 *Cn*, fig. 290, *p*), is a reddish body of about the size of a small cherry-stone, and is named from its supposed resemblance in shape to a fir-cone. It is connected with the posterior part of the third ventricle, projecting backwards and downwards between the superior pair of corpora quadrigemina. It is attached by a broad but flattened stalk which is separated by the recess of the ventricle before mentioned (p. 321) into an upper and under portion, the latter of which curves downwards and passes below into the posterior commissure, while the upper portion extends on either side along the ridge-like junction of the upper and mesial surfaces of the thalamus as the medullary stria or peduncle of the gland (fig. 290, *sp.*) At the sides the stalk passes into the trigonum habenulæ. The pia mater

which invests the mesencephalon, covers the pineal gland with a special investment before being prolonged as the velum interpositum over the third ventricle and thalamus; and the gland is liable to be torn away in removing the pia mater.

In microscopic structure the pineal gland somewhat resembles the anterior lobe of the pituitary body. It is similarly composed of a number of hollow follicles generally spherical, but in some cases tubular, separated from one another by ingrowths of connective tissue. The follicles are almost filled with epithelial cells and often contain, besides corpora amylacea, much gritty calcareous matter (acervulus cerebri, brain sand), composed of microscopic particles, aggregated into masses and formed of earthy salts (phosphate and carbonate of lime, with a little phosphate of magnesia and ammonia) combined with animal matter.

The sabulous matter is frequently found on the outside of the pineal body, or even deposited upon its peduncles. It is found also in the choroid plexuses; and in a scattered form occurs in other parts of the membranes of the brain. It is found at all ages, frequently in young children, and sometimes even in the fœtus. It cannot, therefore be regarded as the product of disease. Huschke has pointed out that the pineal body is larger in the child and the female than in the adult male. In the brains of other mammals it is proportionally larger than in the human subject, and less loaded with brain sand. The pineal body is developed originally as a hollow outgrowth from that part of the embryonic brain which afterwards forms the third ventricle; the diverticulum becoming subsequently cut off from the ventricle, and undergoing ramification to form tubes which are afterwards separated for the most part into isolated vesicles.

The **posterior perforated space** (locus perforatus posticus) (fig. 260, ×) is a deep fossa at the base of the brain, at the bottom of which is greyish matter, connecting the diverging crura. It is perforated by numerous small openings for the passage of blood-vessels; and some horizontal white striæ usually pass out of the grey matter and turn round the peduncles close to the upper border of the pons to reach eventually the medullary centre of the cerebellum (*tænia pontis*). It corresponds posteriorly, as far as a line joining the anterior borders of the third nerves, to the floor of the aqueduct of Sylvius, but in front of those nerves to the posterior part of the floor of the third ventricle. In the grey matter over the space are a few scattered nerve-cells.

The **corpora albicantia** or **mammillaria** (fig. 260, *a*) are two round white eminences in front of this fossa, each about the size of a small pea, connected together across the middle line. Each corpus albicans contains a nucleus of grey matter concealed within its superficial white fibres.

The corpora albicantia are formed, as will hereafter be explained, by the anterior pillars of the fornix; hence they have also been named *bulbs of the fornix*. In most vertebrate animals there is but one median corpus albicans in place of two.

The **tuber cinereum** (figs. 260, 290, *t c*) is a lamina of grey matter extending forwards from the corpora albicantia to the optic commissure, to which it is attached. It forms part of the floor of the third ventricle. In the middle it is prolonged forwards and downwards into a hollow conical process, the **infundibulum** (fig. 292, *i*), to the extremity of which is fixed the pituitary body. On its outer side close to the optic tract is a collection of grey matter with nerve-cells, termed by Meynert the *basal optic ganglion*, from which fibres arise which pass to the optic tract and optic nerve of the same side.

The **pituitary body** or *hypophysis cerebri* (fig. 260, 261, *h*, and fig. 292), formerly called pituitary gland, from its being erroneously supposed to discharge *pituita* into the nostrils, is a small reddish grey mass, of a somewhat flattened oval shape, widest in the transverse direction, and occupying the sella turcica of the sphenoid bone. Its weight is from five to ten grains. It consists of two lobes, of which the anterior is larger, and concave behind, where it embraces the smaller posterior lobe.

The two lobes are entirely different, both in their structure and development; and it is only in mammals that they come into close connexion with one another. The *posterior lobe* is developed as a hollow downgrowth of the part of that cavity of the embryonic brain, which afterwards becomes the third ventricle. In the lower vertebrates, and especially in fishes, the cells which compose its walls become converted into nerve-cells and fibres, and as the *lobus infundibuli* it becomes an integral part of the brain. But in the higher vertebrates it remains

Fig. 292.

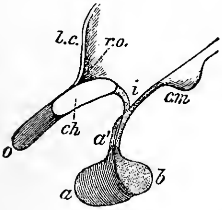


Fig. 292.—Sagittal section of the pituitary body and infundibulum with the adjoining part of the 3rd ventricle (Schwalbe).

a, anterior lobe; *a'*, a projection from it towards the front of the infundibulum, *i*; *b*, posterior lobe connected by a solid stalk with the infundibulum; *l. c*, lamina cinerea; *o*, right optic nerve; *ch*, section of chiasma; *r. o*, recess of the ventricle above the chiasma; *c. m.* corpus mammillare.

small and almost undeveloped; its cavity is obliterated, and all nervous structure becomes obscured by the ingrowth of vessels and of connective tissue into the now solid organ. The connective tissue forms reticulating bundles, between which occur numerous spindle-shaped and branched cells, as well as a few larger corpuscles containing pigment-granules in their protoplasm. Sometimes remains of the original hollow are seen in the form of a cavity lined by columnar ciliated cells.

The *anterior lobe*, darker in colour than the posterior, is developed as a tubular prolongation from the ectoderm of the buccal cavity, with which it is therefore originally in connection, although it soon becomes separated by the growth of intervening tissue. In the adult it is constituted by a large number of slightly convoluted tubules or alveoli, similar to those of a secreting gland, and in like manner lined by epithelium, which in some cases fills up the tubule. The tubules are united by connective tissue, which is especially abundant in the neighbourhood of the larger blood-vessels, and also forms a sort of capsule to the organ. Moreover, portions of the tubules are frequently cut off by the connective tissue so as to form isolated vesicles. The outer layer of epithelium is columnar; and in some of the larger tubes, especially those next to the posterior lobe, cilia may be detected on the cells. The blood-vessels are numerous, and the capillaries form a close network around the walls of the tubules. The lymphatics of the organ originate in cleft-like spaces between the tubules and pass to a network in the capsule. In its microscopic structure the anterior lobe of the pituitary body approaches closely that of the thyroid body, the vesicles of which are also originally a network of anastomosing tubules, and in some animals remain throughout life in this condition. Moreover, a colloid substance like that in the thyroid vesicles, is found sometimes in the alveoli of the anterior lobe of the hypophysis.

The **optic commissure**, or *chiasma* (fig. 260), is constituted by the union of the two optic tracts in front of the tuber cinereum, and from it the two optic nerves proceed. In it the nerve-fibres of the two sides undergo a decussation. Their arrangement in the decussation will be more fully considered when the origin of the optic nerve is described.

In the middle line of the base of the brain, in front of the optic commissure, is the anterior portion of the great longitudinal fissure, which passes down between the hemispheres. At a short distance in front of the chiasma, this fissure is crossed transversely by a white mass, which is the anterior recurved extremity of the corpus callosum. On gently turning back the optic commissure, a thin connecting layer of grey substance, the **lamina cinerea,** is seen occupying the space between the corpus callosum and the chiasma, and continuous above the latter with the tuber cinereum. It is connected at the sides with the grey substance of the anterior perforated space, and forms part of the anterior boundary of the third ventricle (fig. 290, *l c*) : it is somewhat liable to be torn in removing the brain from the skull ; and, in that case, an aperture would be made into the fore part of the third ventricle.

THE CEREBRAL HEMISPHERES.

EXTERNAL CONFORMATION.

The **cerebral hemispheres** together form an ovoid mass, flattened on its under side, and placed in the cranium with its smaller end forwards, its greatest width being opposite to the parietal eminences. They are deeply separated in a large part of their extent by the great longitudinal fissure.

Fig. 293.

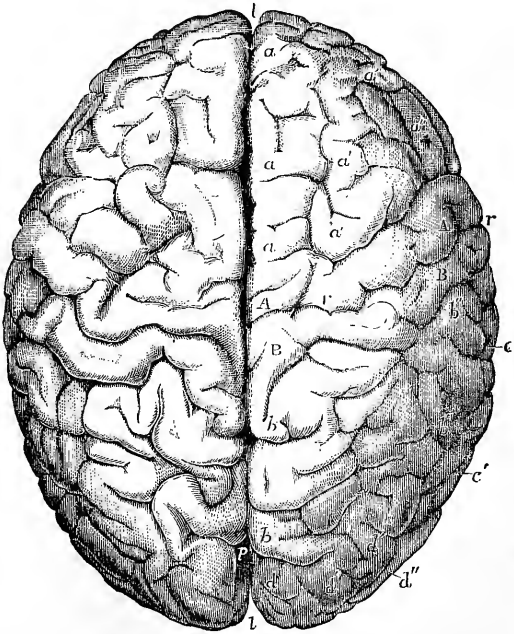


Fig. 293.—Upper surface of the brain showing the convolutions (from R. Wagner). ½

This view was taken from the brain of Professor C. F. Gauss, the mathematician, who died in 1854, aged 78. It is selected as an example of a well-formed brain of the average size with fully developed convolutions.

a, *a*, *a*, superior or first frontal convolution ; *a′*, *a′*, *a′*, second or middle frontal ; *a″*, third or inferior frontal ; A, A, ascending frontal convolution ; B, B, ascending parietal convolution ; *b*, superior parietal lobule ; *b″*, inferior parietal lobule ; *c*, first or upper temporo-sphenoidal convolution ; *d*, first or upper occipital convolution ; *d′*, second or middle ; *d″*, third or lower ; *l*, *l*, the longitudinal fissure ; *r*, the sulcus of Rolando ; *p*, the external parieto-occipital fissure (which appears, in consequence of the position of the brain, nearer to the posterior extremity than it really is).

Each cerebral hemisphere has an outer, convex surface, in contact with the vault of the cranium ; an inner or median, flat surface, which forms one side of the longitudinal fissure ; and an irregular under surface, in which is a deep cleft, the fissure of Sylvius. In front of this cleft the under surface rests in the anterior fossa of the base of the skull, and behind it in the middle fossa, and further back still, on the tentorium cerebelli.

The **great longitudinal fissure** (fig. 293, *l l*), seen upon the upper surface of the brain, extends from before backwards throughout its whole length in the median plane, and thus separates the cerebrum, as already stated, into a right and left hemisphere. On opening this fissure, it is seen, both before and behind, to pass quite through to the base of the cerebrum ; but in the middle it is interrupted by a large transverse mass of white substance, named the *corpus callosum* or great commissure, which connects the two hemispheres together. While the brain is within the skull, this fissure is occupied by a vertical process of the dura mater —the falx cerebri—which dips down between the two hemispheres, not quite reaching to the corpus callosum in front but touching it behind.

At a short distance beneath the anterior recurved end of the corpus callosum and outwards from the lamina cinerea there is seen at the base of each hemisphere the **anterior perforated space** (locus perforatus anticus), a depression near the entrance of the Sylvian fissure, floored with grey matter, and pierced with a multitude of small holes for the passage of blood-vessels, most of which are destined for the corpus striatum, beneath which it lies, and which here comes to the surface.

The grey surface of each perforated space is crossed by a broad white band, which may be traced from the corpus callosum, backwards and outwards along the side of the lamina cinerea towards the entrance of the Sylvian fissure. These bands of the two sides are named the *peduncles of the corpus callosum.*

The surface of the hemispheres is composed of grey matter, and is moulded into numerous smooth and tortuous eminences, named *convolutions* or *gyri,* which are marked off from each other by *furrows* or *sulci* of varying depth.

The convolutions are covered closely throughout by the vascular investing membrane, the pia mater, which sends processes down to the bottom of the sulci between them, while the arachnoid membrane passes from one convolution to another, without dipping between them. In general, the depth of a convolution exceeds its thickness ; and its thickness, near the summit, is somewhat greater than through its base. The convolutions present considerable variations of position, direction and complexity in the brain of different individuals, and even in the two sides of the same brain.

Since the external grey or cortical substance is continuous over the whole surface of the cerebral hemispheres, being found alike within the sulci and upon the gyri, it is obvious that a far greater extent of grey matter is thus exposed to the vascular surface of the pia mater with a given size of the brain, than could have been the case had the hemispheres been plain and destitute of convolutions.

The sulci between the convolutions are generally from half an inch to an inch in depth, but vary in this respect both in different brains and in different parts of the same brain. In general certain well-marked furrows

can easily be recognised, which have been regarded as separating the surface of the hemispheres into five lobes.

The lobes are termed respectively *frontal, parietal, occipital, temporo-sphenoidal* and *central*. The three former are in contact with the bones after which they are named, though their limits do not correspond to those of the bones ; the fourth occupies the middle or temporo-sphenoidal fossa in the base of the skull, while the central lobe or island of Reil, which in the embryo is the first part to be formed, lies concealed by parts of the others, which have grown over it in the course of development. The divisions between these lobes will be better understood when the convolutions and sulci have been described.

Formerly it was customary to divide each hemisphere into three lobes, an anterior, in front of the fissure of Sylvius, a middle, behind that fissure and resting in the temporo-sphenoidal fossa, and a posterior lobe behind it, resting on the tentorium cerebelli. The division into five lobes, now generally adopted, was first made by Gratiolet.

To the five lobes above enumerated must be added a sixth, viz. : the *olfactory lobe*. This, often erroneously named *olfactory nerve*, appears in man only in the form of a slender process of the brain with a bulbous termination, lying along the under surface of the frontal lobe, but in most animals it is a well developed part of the cerebral hemisphere.

It is convenient to make a distinction between those sulci which when first seen in the embryo appear as infoldings of the whole thickness of the wall of the vesicle of the cerebral hemispheres and those that only involve the superficial parts of the hemisphere and as a rule make their appearance later. Of the former there are five in all, viz., the Sylvian, the parieto-occipital, the calcarine, the collateral, and the hippocampal. These *complete sulci* are characterized by the fact that they correspond to prominences seen in the ventricles of the hemispheres, whereas the other furrows are generally of less depth, their situation in most cases having been determined by the course of the blood-vessels, and they present no indication internally. In the description we shall follow Pansch in reserving the designation "fissures" for the complete sulci.

Interlobar sulci.—These are three in number, viz. :—the fissure of Sylvius, the sulcus of Rolando, and the parieto-occipital fissure.

The *fissure of Sylvius* (fig. 294) commences at the outer side of a depression the bottom of which is formed by the anterior perforated space, and which is distinguished as the *vallecula Sylvii*. From this place it passes transversely outwards to the lateral surface of the hemisphere, where it divides into a short anterior ascending limb, and a longer posterior horizontal limb. On the under surface the fissure is a deep cleft of which the posterior lip is more prominent than the anterior.

The anterior or ascending limb (*f. Sy. a*), not quite an inch in length, runs upwards and forwards into the frontal lobe, the lowest convolution of which curves round it. Its end is generally bifid.

The posterior or horizontal limb (*f. Sy. p*) passes backwards between the parietal and temporo-sphenoidal lobes, ascending slightly, through about the middle third of the hemisphere. Its extremity is usually bent upwards, and passes into the parietal lobe.

The group of convolutions which occupies the angle between the two divisions of the fissure of Sylvius, has been collectively termed the *operculum of the insula* (Broca). By turning the operculum forcibly upwards, the fissure of Sylvius is opened up and the central lobe comes into view.

The *furrow of Rolando* or *central sulcus* (fig. 296, *f. Ro.*; and fig. 293, *r*), extends across the lateral convex surface of the hemisphere interrupting the general longitudinal course of the gyri and sulci. It commences above, near the vertex, close to the great longitudinal fissure, and passes downwards and forwards to end a little behind the bifurcation of the fissure of Sylvius, into the posterior limb of which it sometimes but very rarely opens. Its position and direction are such that the fissures of the two sides, seen from above, form a wide V-shaped figure, open in front. It is rarely interrupted in its course, appears early in fœtal life (end of the fifth month), and is very uniform in man and in the Quadrumana of the old world, but is not present in mammalia generally. It is apparently caused by a venous communication between the superior longitudinal sinus and the middle cerebral vein, which is well marked in the fœtus from the fourth to the sixth month, but afterwards becomes atrophied (W. Krause).

This furrow separates the frontal from the parietal lobe. The parallel convolutions which bound it are named respectively the ascending frontal and ascending parietal convolutions.

It is in the immediate neighbourhood of this sulcus that the chief of the so-called motor areas of the cerebral cortex are situated.

Fig. 294.

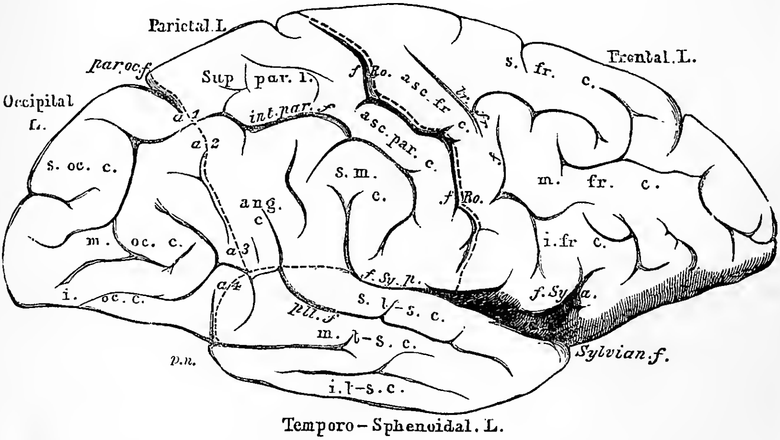


Fig. 294.—Convolutions of outer surface of right hemisphere. From a simply-convoluted European brain. About half the natural size (W. R. Gowers).

The convolutions are, for the most part, indicated by Roman, the furrows by italic letters. The dotted lines indicate the divisions into lobes, the names of which are given in full at the margin of the hemisphere. *f. Ro.*, furrow of Rolando; *par.-oc. f.*, parieto-occipital fissure; *f. Sy. a.*, anterior limb, and *f. Sy. p.*, posterior limb, of the fissure of Sylvius: s.fr.c., m.fr.c., i.fr.c., superior, middle, and inferior frontal convolutions; asc.fr.c., ascending ditto; asc.par.c., ascending parietal convolution; sup.par.l., superior parietal lobule; s.m.c., supra-marginal convolution; ang.c., angular convolution; *int. par. f.*, intra-parietal furrow; s.oc.c., m.oc.c., i.oc.c., superior, middle, and inferior occipital convolutions; *p. n.* præ-occipital notch; s.t.-s.c., m.t.-s.c., i.t.-s.c., superior, middle, and inferior temporo-sphenoidal convolutions *pll. f.*, parallel furrow; a^1, a^2, a^3, a^4; first, second, third and fourth annectant convolution; c. l., within the fissure of Sylvius, central lobe, or Island of Reil.

The *parieto-occipital fissure*, is best marked on the median surface of the hemisphere, where it appears as a deep cleft (fig. 297), extending downwards and a little forwards from the margin of this surface to near the posterior extremity of the corpus callosum. On the convex surface it is continued transversely outwards for a variable distance, generally much less than an inch, as the *external parieto-occipital fissure* (fig. 294, *par. oc. f.*) This fissure is taken as the division between the parietal and occipital lobes. The size of its external portion depends (inversely) on the size of the convolution which curves round its outer extremity and connects the parietal with the occipital lobe. In consequence of the development in man of this and similar connecting convolutions, this fissure is much less marked in the human brain than in that of the higher apes (fig. 295). It appears about the fourth or fifth month.

Fig. 295.

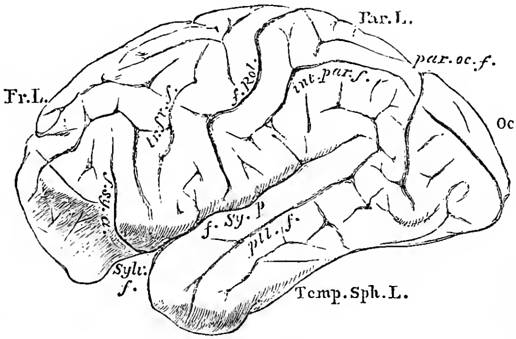


Fig. 295.—Brain of Chimpanzee (from Gratiolet).

Fr. L., frontal lobe; Par.l., parietal lobe; Oc.L., occipital lobe; Temp. Sph. L., temporo-sphenoidal lobe; *Sylv.f.*, fissure of Sylvius; *f.Sy.a.*, *f.Sy. p.*, its anterior and posterior limbs; *f. Rol.*, furrow of Rolando; *tr.fr.f.*, transverse frontal furrow; *int-par.f.*, intra-parietal furrow; *par.-oc.f.*, parieto-occipital furrow.

The Lobes of the External Surface, with the Intralobular Gyri and Sulci.—The **Central Lobe**, or **Island of Reil** (*insula*) (fig. 296), lies deeply within the commencement of the fissure of Sylvius, being rarely visible except when the lips of that fissure are separated. It is a triangular eminence, and consists of five or six short, straight convolutions (gyri operti) which radiate outwards from a point just external to the anterior perforated spot. Externally it is separated by a deep sulcus (*external sulcus* of Reil) from the contiguous convolutions of the *operculum*, *i.e.*, the extremity of the ascending parietal, ascending frontal, and inferior frontal convolution. Anteriorly it is limited by a nearly transverse sulcus (*anterior sulcus* of Reil) which runs from the vallecula into the anterior limb of the fissure of Sylvius, and serves to separate the island from the posterior orbital convolution of the frontal lobe, except mesially. Posteriorly it is also bounded by a deep groove (*posterior sulcus* of Reil) which runs from the vallecula into the posterior limb of the fissure of Sylvius and separates the island from the upper surface of the temporo-sphenoidal lobe. The island of Reil covers the lenticular nucleus of the corpus striatum. It appears earlier than any other division of the cerebrum, both in the fœtus and in the animal series, and is at first,

therefore, prominent; but it becomes gradually covered in by the parts of the hemisphere which are subsequently developed.

Olfactory lobe.—From the front of the anterior perforated spot a nerve-like process extends—the olfactory tract (fig. 296, *olf.t.*). It is lodged in a hollow (olfactory sulcus) in the under (orbital) surface of the frontal lobe of the cerebral hemisphere, close to the longitudinal fissure. It ends in front in an oval swelling—the olfactory bulb, which consists chiefly of grey substance, and gives origin to the small nerves which proceed, through the foramina of the ethmoid bone, to the nose. Traced backwards, the olfactory tract bifurcates near the front of the anterior perforated space, and is continued into two divergent white bands or striæ, which are known as its roots. The *outer* root

Fig. 296.

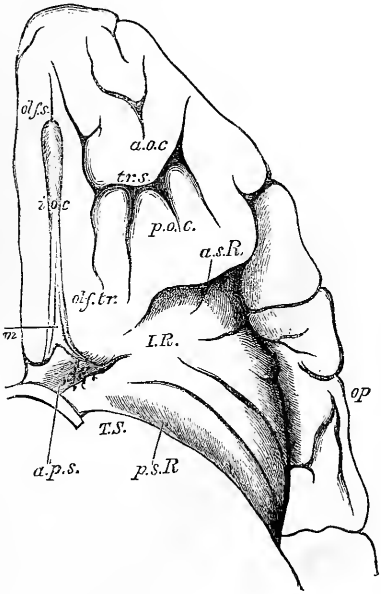


Fig. 296.—Orbital surface of the frontal lobe, and island of Reil. Natural size. (Turner).

The island (*I.R.*) is exposed by removal of the apex of the temporo-sphenoidal lobe. *T.S.*, cut ridge of this lobe; *a.p.s.*, anterior perforated space; *a.s.R.*, *p.s.R.*, anterior and posterior limiting sulci of the island; *op*, operculum of the island. *tr.s.*, tri-radiate sulcus; *i.o.c.*, *a.o.c.*, and *p.o.c.*, internal, anterior, and posterior orbital convolutions; *olf.s.*, end of the olfactory sulcus; *olf.tr.*, olfactory tract, bifurcating behind into the two roots inner and outer; *m*, middle root or tuber olfactorium.

passes, as a white streak, outwards and backwards along the anterior margin of the perforated space, towards the Sylvian fissure, where it disappears from the surface. The *inner* root passes obliquely inwards to the side of the great longitudinal fissure between the hemispheres. Between the two roots a triangular area of grey matter is enclosed, which is continuous behind with the grey matter of the anterior perforated lamina. The area in question forms the base of a small pyramidal lobule, named the *tuber olfactorium*, which is received into a corresponding depression on the under surface of the frontal lobe, with the grey cortex of which it is continuous. It is composed of white substance internally, which is in continuity above with that of the frontal lobe, and anteriorly with the olfactory tract.

This olfactory tubercle is often described as the *middle or grey root* of the olfactory tract: and white fibres are sometimes prolonged from that tract over its surface and pass to the anterior perforated lamina.

The **Frontal Lobe** is the portion of the brain in front of the furrow of Rolando, and above and in front of the fissure of Sylvius. On the

median surface there is no corresponding demarcation, unless the calloso-marginal furrow is regarded as forming a boundary to the lobe on this surface. The inferior surface of the frontal lobe, which is in contact with the orbital plate, is called the *orbital surface ;* the upper arched aspect is the *frontal surface.*

Convolutions and furrows on the frontal surface.—The convolutions of the frontal lobe on the frontal surface, are four in number, three antero-posterior, one above the other, and one transverse behind them.

The *transverse* or *ascending frontal convolution* (fig. 294, asc. fr. c., fig. 293 A.A.) (anterior central convolution) is placed in front of the furrow of Rolando, which it thus bounds. Below, it commences a little behind the bifurcation of the fissure of Sylvius, and thence courses upwards and backwards to the margin of the great longitudinal fissure. Its prolongation on the median surface of the hemisphere forms part of the paracentral lobule. It is commonly connected above, and almost invariably below, with the convolution (ascending parietal) behind the furrow of Rolando, and thus that sulcus is isolated.

The portion of the frontal surface anterior to this convolution is occupied by complex gyri running more or less in an antero-posterior direction, and usually to be distinguished into three, an upper, middle, and lower. These are generally continuous superficially with the ascending frontal ; and they are usually in their course connected one with another by secondary convolutions. They are as follows :—

The *superior frontal convolution* (s. fr. c.), situated at the margin of the great longitudinal fissure, commences generally at the upper end of the ascending frontal, and extends to the anterior extremity of the hemisphere, where it passes over to the orbital surface and becomes the inner convolution. The inner aspect of this convolution appears on the median surface of the hemisphere, where it is known as the marginal convolution.*

The *middle frontal convolution* (m. fr. c.) arises deeply or superficially from the ascending frontal below the last, and running forwards turns round the margin of the lobe to become continuous with the middle orbital. It is usually broad, and often much subdivided.

The *inferior frontal convolution* (i. fr. c.) forms the lower and outer portion of the frontal lobe. It arises from the lower extremity of the ascending convolution, just above the bifurcation of the fissure of Sylvius, arches round the ascending limb of that fissure, and passes on to the inferior surface of the hemisphere, as the posterior orbital gyrus.

The *transverse frontal furrow* (*tr. fr.*) (præcentral sulcus) lies in front of the ascending frontal convolution, and parallel to the lower half of the furrow of Rolando. Its extent depends on the mode of origin of the middle and inferior frontal convolutions from the ascending frontal. When these arise superficially the furrow is interrupted, and may be inconspicuous ; when the inferior frontal convolution arises deeply, this furrow is continuous with the fissure of Sylvius, and it has, in consequence, been regarded as the prolongation of the ascending limb of that fissure.

Two *antero-posterior sulci,* the *superior* and *inferior frontal,* separate

* It will be convenient to defer the complete description of the convolutions which appear on the median surface, until that surface is considered as a whole.

the corresponding convolutions from the middle frontal: they are often very irregular, being bridged over by secondary convolutions.

Convolutions and furrows on the orbital surface (fig. 296).—The *orbital* or *tri-radiate sulcus* lies in the centre of this surface of the lobe, and usually has three arms, one passing forwards, one curving outwards, and another backwards and inwards.

Three convolutions are described as lying around the orbital sulcus, and named according to their position, the *inner*, the *anterior*, and the *posterior* or *outer*. The last of these is continuous at the side with the inferior frontal, the first and second are the continuations of the superior and middle frontal convolutions.

On the inner gyrus is seen the *olfactory sulcus* in which the olfactory tract and bulb lie. It has a straight course parallel with and near the great longitudinal fissure.

The **Parietal Lobe** lies behind the frontal and in front of the occipital lobe. The temporo-sphenoidal lobe is below it. It is bounded in front by the sulcus of Rolando, behind by the parieto-occipital fissure, and by a continuation of the line of that fissure to the lateral boundary. It is limited by the posterior limb of the fissure of Sylvius as far as this preserves its horizontal direction, and then by a line continuing that direction to the posterior boundary, but above and mesially it extends within the great longitudinal fissure and appears on the inner side of the hemisphere.

Sulci and gyri of the parietal lobe.—The *intraparietal sulcus* (fig. 294, *int. par. f.*) arches through the parietal lobe, commencing in its anterior inferior angle, where it is sometimes, though rarely, continuous with the fissure of Sylvius. It ascends at first parallel to the furrow of Rolando, and then turns backwards horizontally to the back of the lobe, extending nearly to the termination of the external parieto-occipital fissure, past which it is often continued into the occipital lobe. Its horizontal portion divides the parietal lobe into two parts, the superior and inferior parietal lobules, and it is frequently bridged across by a secondary convolution connecting those lobules.

The *ascending parietal* (or posterior central) *convolution* (fig. 293, B, B, fig. 294, asc. par. c.) lies behind the sulcus of Rolando, and parallel to the ascending frontal convolution, with which it is usually continuous, both above and below, the connection below being larger than that above. In its lower half the ascending parietal convolution lies in front of the anterior part of the intraparietal sulcus. Above, it is continuous with the superior parietal convolution.

The *superior parietal convolution or lobule* (fig. 294, sup. par. l.) is that part of the parietal lobe which lies above the intraparietal sulcus, and behind the upper part of the last described convolution, from which it is imperfectly separated by a slightly marked groove (postcentral sulcus) which is sometimes a branch of the intraparietal. Its posterior limit is the boundary of the parietal lobe, viz., the external parieto-occipital fissure, outside the extremity of which a narrow convolution usually connects this lobule with the occipital lobe, and is termed the first connecting or annectant convolution. The superior parietal is continuous on the mesial surface of the hemisphere with the quadrate lobule.

The *inferior parietal lobule* lies behind the ascending and below the horizontal part of the intraparietal sulcus. It is divided into two, a supramarginal gyrus, above and in front of the extremity of the

Sylvian fissure, and an angular gyrus behind it. The *supramarginal convolution* (s.m.c.) lies behind the lower end of the intraparietal sulcus, beneath which it is usually continuous with the ascending parietal convolution. It arches over the upturned extremity of the fissure of Sylvius, and becomes continuous with the superior temporo-sphenoidal convolution. The *angular gyrus* (ang. c.) is connected in front with the supramarginal, bends over the end of the parallel sulcus, and is continued downwards into the middle temporo-sphenoidal convolution. Behind it is connected with the occipital lobe by means of one or two (second and third) annectant convolutions.

The **Occipital Lobe** of pyramidal shape, lies behind the parietal, and forms with its rounded apex the posterior extremity of the hemisphere. At its lower and fore part, it is continuous with the temporo-sphenoidal lobe. It occupies the superior fossa of the occipital bone, and rests on the tentorium. Its limits are in some degree artificial. In front it is bounded by the external parieto-occipital fissure, and by a line continuing the direction of the fissure across the annectant convolutions to meet the inferior boundary of the parietal lobe, and thence prolonged to the lower edge of the external surface of the hemisphere at the anterior edge of the tentorium. There is generally a notch (præ-occipital notch, fig. 294, *p. n.*) at this lower border, and a curved line extending from this notch to the parieto-occipital fissure, would mark off the lobe externally, often coinciding for a short distance with an oblique furrow which may be found running between it and the temporo-sphenoidal lobe.

Convolutions and furrows of the occipital lobe.—On the dorsal surface three convolutions are commonly described, *superior, middle, and inferior* (fig. 294). They are continuous with the convolutions of the parietal and temporo-sphenoidal lobes by the four *annectant* or connecting *convolutions*, of which the *first*, passing round the extremity, or in rare cases deeply across the bottom, of the external parieto-occipital fissure, connects the superior occipital convolution with the superior parietal lobule, the *second* unites the middle occipital and angular convolutions, the *third* connects the middle occipital with the lower end of the angular or the middle temporo-sphenoidal, and the *fourth* connects the inferior occipital with the inferior temporo-sphenoidal convolution (a^1, a^2, a^3, a^4). The three occipital convolutions are separated by two furrows, the *superior and middle occipital*, of which the superior is often continuous with the intraparietal. There is also generally a small groove directed outwards across the upper part of the occipital lobe a little behind the parieto-occipital fissure. This is named the *transverse occipital sulcus*, and represents the outer portion of the external perpendicular fissure of the ape's brain.

At the lateral edge of the lobe is another furrow, the *inferior occipital*, which serves to separate the inferior occipital convolution from the occipito-temporal on the under surface of the lobe. The superior occipital convolution on the other hand has no sulcus bounding it at the mesial edge of the hemisphere, but passes continuously into the cuneate lobule on the mesial surface.

On the mesial (under) surface of the occipital lobe are the posterior parts of the *occipito-temporal convolutions*, which, as well as the furrows separating them, will be described with the convolutions of the inner surface of the hemisphere.

The longitudinal venous sinus in passing downwards causes an impression on the posterior surface of the occipital lobe, at the mesial border (Bastian). This impression is generally found on the right side, but sometimes on the left.

The **Temporo-sphenoidal lobe** is bounded in front and above by the commencement and posterior limb of the fissure of Sylvius. Behind, it is continuous with the occipital lobe, and above with part of the parietal lobe. It is somewhat pyramidal in shape, having three surfaces, viz., lateral, superior and inferior, the last concealed within the fissure of Sylvius. The rounded apex of the pyramid is free, and lies in front beneath the orbital surface of the frontal lobe from which it is separated by the broad commencement of the Sylvian fissure.

Sulci and gyri of the temporo-sphenoidal lobe.—The upper surface of this lobe is marked by two or three *transverse temporal gyri* (Heschl). On the lateral and under surfaces there are three sulci with an antero-posterior direction. The first or *superior temporo-sphenoidal sulcus*, also termed from its relation to the Sylvian fissure the *parallel sulcus* (*pll.f.*), is an important furrow, appearing in the sixth month, and being constant in the Primates. It is sometimes interrupted by a small gyrus connecting the convolutions above and below it. The *middle temporo-sphenoidal sulcus* runs parallel to and below the last but is far less constant in extent and direction. It is also generally interrupted by a vertical connecting gyrus. The *inferior temporo-sphenoidal sulcus* is seen on the under surface of the lobe extending behind nearly to the pre-occipital notch.

Three nearly parallel convolutions can usually be distinguished on the lateral surface of this lobe ; a *superior* (inframarginal (fig. 294, s. t-s. c.)) bounding below the posterior limb of the Sylvian fissure, and continuous behind with the supramarginal and to a less extent with the angular convolution of the parietal lobe, a *middle* (m. t-s. c.) continuous with the angular gyrus, and with the middle occipital convolution by means of the third annectant gyrus, and an *inferior* (i. t-s. c.) continuous with the inferior occipital through the fourth annectant gyrus.

The anterior parts of the two *occipito-temporal convolutions* (the posterior parts of which belong to the occipital lobe) are seen on the under or mesial surface of the temporo-sphenoidal lobe. They are separated by the collateral fissure.

Gyri and sulci on the mesial and tentorial surfaces of the hemisphere (fig. 297). The following furrows and convolutions are seen on this surface :—

The *calcarine fissure* (fig. 297, *calc.f.*) commences by a forked end near the posterior extremity of the hemisphere, and extends forwards, being joined about half way in its course by the internal parieto-occipital, to terminate a short distance beneath the posterior extremity of the corpus callosum. It corresponds to the projection of the hippocampus minor (calcar avis) in the posterior cornu of the lateral ventricle.

The *calloso-marginal sulcus* (*c. m.f.*) commences beneath the anterior extremity of the corpus callosum, and courses first forwards, then upwards, and then backwards, parallel with the edge of the longitudinal fissure ; finally it turns obliquely or vertically upwards to end at this edge a short distance behind the upper extremity of the sulcus of Rolando. It separates the marginal convolution from the convolution of the corpus callosum.

The *hippocampal* or *dentate fissure* (*d.f.*) commences within the posterior

extremity of the gyrus fornicatus, which separates it from the end of the calcarine fissure. Thence it extends downwards and forwards, ending below in the notch of the uncinate convolution. This fissure corresponds to the elevation of the hippocampus major in the floor of the lateral ventricle.

The *internal parieto-occipital fissure* (*par-oc. f.*) is a large and deep sulcus which extends downwards and forwards to join the calcarine fissure. It assists the calcarine in forming the projection into the lateral ventricle known as the calcar avis.

The *collateral fissure* (occipito-temporal, *coll.f.*) is so named from the fact that extending deeply into the substance of the hemisphere it projects in the descending cornu of the lateral ventricle as the *eminentia collateralis.* It runs between the superior and inferior occipito-temporal convolutions.

The *cuneate lobule* (occipital lobule) is a wedge-shaped area lying between the internal parieto-occipital and the calcarine fissures. As already stated it is the mesial part of the superior occipital convolution.

Fig. 297.

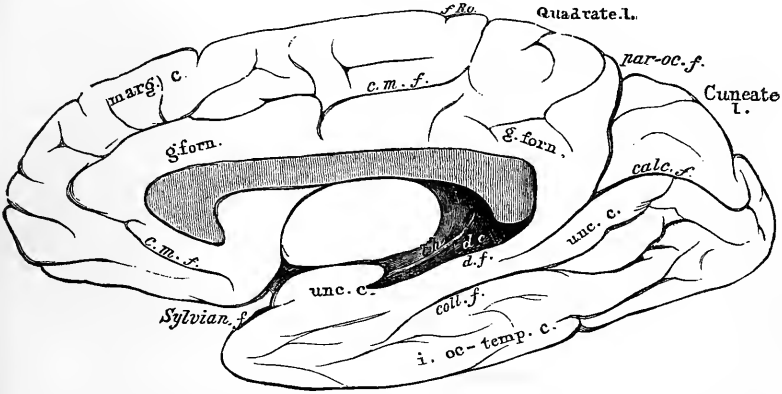


Fig. 297.—Convolutions of the mesial and tentorial surfaces of the right hemisphere. From a simply convoluted European brain. About half the natural size. (Gowers.)

Marg. c., marginal convolution ; *g. forn.*, gyrus fornicatus or convolution of the corpus callosum ; *unc. c.*, uncinate convolution ; *i. oc.-temp. c.*, inferior occipito-temporal convolution : *d. c.*, dentate convolution ; *f. Ro.*, depression corresponding to the upper extremity of the furrow of Rolando ; *par.-oc. f.*, parieto-occipital fissure ; *calc. f.*, calcarine fissure ; *coll. f.*, collateral fissure ; *d. f.*, dentate fissure ; *t. h.*, tænia hippocampi.

The *quadrate lobule* (præcuneus) is a four-sided area lying between the internal parieto-occipital fissure behind, and the termination of the calloso-marginal fissure in front. It is variously subdivided into small gyri, and is continuous above with the superior parietal lobule, and below with the gyrus fornicatus. The quadrate lobule belongs to the parietal lobe of the hemisphere.

The *marginal convolution* (marg. c.) commences in front of the anterior perforated spot, and extends along the edge of the longitudinal fissure as far as the termination of the calloso-marginal fissure at the upper margin of this surface. Over this margin it is continuous with the dorsal part of the superior frontal convolution, and with the continuation of this on the orbital surface. It is commonly broken up by secondary sulci, one

of which often runs parallel to part of the calloso-marginal sulcus. A secondary convolution not uncommonly connects it with the next gyrus.

The *convolution of the corpus callosum* or *gyrus fornicatus* (g. forn., fig. 297), commences near the anterior perforated spot, and, turning round the anterior extremity of the corpus callosum, runs backwards along its upper surface, and then, bending down behind its posterior extremity, becomes continuous with the uncinate convolution. It is bounded in front and superiorly for about two-thirds of its extent by the calloso-marginal fissure. Between it and the corpus callosum is a well marked groove—the furrow of the corpus callosum. The hinder part of the gyrus fornicatus is connected above with the quadrate lobule, and joins below the uncinate convolution.

The *dentate convolution* (fascia dentata, fig. 297, d c, fig. 298, *c*), lies within the fissure of the same name. It is so termed from the notched appearance it presents in its lower part. It here forms the limit of the superficial grey matter of the hemisphere, for immediately above it is the white fimbria or tænia hippocampi (*t h*) prolonged from the fornix, and above this again the invagination of the pia mater with its choroidal plexus into the lateral ventricle of the hemisphere. Both fascia dentata and fimbria blend in front with the uncus. In some animals this convolution is much better developed than in man, in whom it is comparatively rudimentary

Fig. 298.

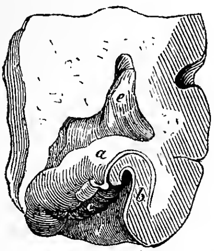


Fig. 298.—Section of the right hippocampus major to show the arrangement of the grey and white substance (from Mayo).

a, white layer on the surface of the hippocampus ending in the fimbria ; *b*, grey substance of the hippocampus ; *c*, fascia dentata ; *d*, uncinate convolution ; between *c* and *d* dentate fissure ; *e*, placed on the eminentia collateralis within the cavity of the lateral ventricle.

The *superior occipito-temporal* or *uncinate convolution* extends forwards from near the posterior end of the hemisphere to within a short distance of the apex of the temporo-sphenoidal lobe. Anteriorly it is bent sharply up into a hook-like extremity (*uncus*). Beneath the posterior extremity of the corpus callosum this convolution is joined by a narrow part (isthmus) of the gyrus fornicatus. Above are the hippocampal and calcarine fissures, whilst the collateral fissure runs below it. The grey matter of the anterior half of this gyrus is covered by a reticular layer of white substance derived from the tænia of the corpus callosum. The part below the calcarine fissure is sometimes distinguished by the name of the *lingual lobule.*

The *inferior occipito-temporal convolution* is of considerable length, extending from the apex of the temporo-sphenoidal lobe backwards to near the posterior extremity of the hemisphere. It lies between the collateral fissure and the inferior temporo-sphenoidal sulcus.

Limbic lobe.—Most of the convolutions on the inner surface of the hemisphere can be referred to one or more of the lobes marked out on the external or dorsal surface. But this is not the case with the gyrus fornicatus and its prolongation the anterior part of the uncinate gyrus, which are for the most part well marked off in nearly all mammals from the surrounding convolutions. For

this and other reasons they have been regarded by Broca as constituting a distinct lobe of the hemisphere (grand lobe limbique).

To the parts included in this lobe of Broca Schwalbe adds the other central parts of the mesial wall of the hemisphere, viz., the lamina septi lucidi and the dentate convolution, as well as the fornix which may be said to unite them; looking upon these as representing an inner encircling convolution concentric with the gyrus fornicatus and uncinatus, and naming the whole lobe thus constituted, the "falciform lobe."

It is worthy of note that the two ends of the limbic lobe of Broca, which are separated by the deep part of the Sylvian fissure, are indirectly united with one another by the roots of the olfactory tract, so that the olfactory lobe, of which this forms a part, is in intimate connection with the limbic lobe. This connection is much more conspicuous in animals.

RELATION OF THE CEREBRAL FISSURES AND CONVOLUTIONS TO THE CRANIAL SUTURES.

This relation was first determined exactly by Broca, and subsequently has been more extensively mapped out by Turner and Hefftler. Broca inserted pins through the cranium at particular points in the cranial sutures, and noted the situation of the chief fissures with reference to the parts of the cerebral surface pierced by the pins. Turner's method consisted in carefully removing successive portions or regions of the cranial wall, and delineating upon the removed parts the fissures which were exposed by their removal.

The most important facts which have been determined by these

Fig. 299.

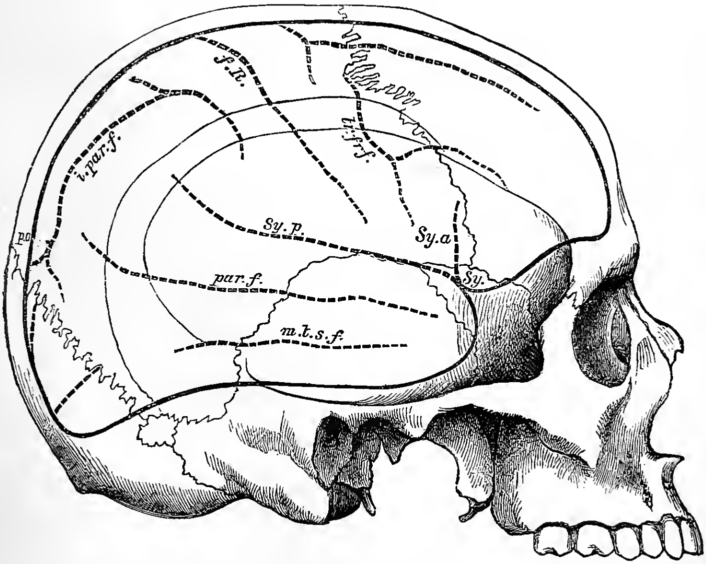


Fig. 299.—Outline sketch of the skull, with the position of some of the principal cerebral sulci marked upon it (from a drawing by G. D. Thane). ½

Sy, Sylvian fissure; *Sy.a.*, *Sy.p.*, its anterior and posterior limbs; *f.R.*, furrow of Rolando; *tr.fr.f.*, transverse frontal furrow; *i.par.f.*, intraparietal furrow; *p.o.*, position of the parieto-occipital fissure; *par.j.* parallel furrow; *m.t.s.f.*, middle temporo-sphenoidal furrow.

methods refer to the Sylvian fissure, the parieto-occipital fissure, and the sulcus of Rolando.

The Sylvian fissure.—The commencement of this nearly corresponds with the suture which unites the anterior inferior angle of the parietal bone with the great wing of the sphenoid. From this point the anterior limb passes up for a short distance nearly parallel with and close to the coronal suture, whilst the posterior limb runs at first along the line of the squamous suture, but afterwards, as this arches downwards, is continued beyond it, curving slightly upwards towards the middle of the parietal bone.

The **parieto-occipital fissure** generally corresponds to the upper end of the lambdoidal fissure, being on a level with the *lambda* (see Vol. I., p. 80).

The **sulcus of Rolando** runs behind the coronal suture, but separated from it by a considerable interval. It is not exactly parallel to the suture, being about one and a half to two inches from it above, and approaching nearly to a distance of one inch from it towards the lower end.

The usual position of several of the other sulci of the outer surface is indicated in the accompanying figure.

INTERNAL PARTS OF THE CEREBRAL HEMISPHERES.

The anatomy of the interior of the cerebrum is most conveniently studied, after the manner of Vieussens and Vicq-d'Azyr, by removing successive portions of the hemispheres by horizontal sections, beginning from above.

The first horizontal section, to be made about half an inch above the corpus callosum, displays the internal white matter of each hemisphere, speckled with red spots where its blood-vessels have been divided, and surrounded on all sides by the grey matter, which is seen to follow closely the convoluted surface. This white central mass in each hemisphere was named by Vicq-d'Azyr *centrum ovale minus*.

Another section being made at the level of the corpus callosum, the white substance of that part is seen to be continuous with the internal medullary matter of both hemispheres: and the large white medullary mass thus displayed, surrounded by the border of cortical substance, constitutes what is generally described as the *centrum ovale of Vieussens*.

The **corpus callosum** or **great commissure** (trabs cerebri) (fig. 300), a white structure which connects the two hemispheres throughout nearly half their length, approaches closer to the front than the back of the hemispheres. It is about an inch in width behind, and somewhat narrower in front. Its thickness is greater at the ends than in the middle, and is greatest behind, where the commissure is nearly half an inch thick. It is arched from before backwards, its lower surface being concave and its upper surface convex. Its upper surface is distinctly marked by transverse furrows, which indicate the direction of the greater number of its fibres. It is also marked in the middle by a longitudinal furrow (*raphe*), which is bounded by two white tracts, placed close to each other, named the *mesial longitudinal striæ* (fig. 300, 3). On each side, near the margin, are seen other longitudinal lines (*lateral longitudinal striæ* or *tæniæ tectæ*) occasioned by scanty white fibres, which form part of a larger bundle lying in the substance of the hemisphere.

In front, the corpus callosum is reflected downwards and backwards, forming a bend named the *genu* (fig. 258). The inferior or reflected portion, which is named the *rostrum*, becomes gradually narrower as it descends, and is connected with the lamina cinerea. It gives off also two bands of white substance, the *peduncles* of the corpus callosum, which, diverging from one another, run backwards across the anterior perforated space on each side to the entrance of the Sylvian fissure (see p. 330). These peduncles traced upwards around the genu are found to be continued into the mesial longitudinal striæ, which posteriorly pass in a divergent manner into the occipital lobes.

Behind, the corpus callosum terminates in a free thickened border, named the *splenium.*

The under surface of the corpus callosum is connected behind with the fornix, a structure to be presently described, and in the rest of its length with the septum lucidum, a vertical partition between the two lateral ventricles, which is included in the anterior bend of the corpus callosum. On the sides the corpus callosum roofs in the body and anterior cornu of the lateral ventricles. The enlarged posterior part or splenium lies over the mesencephalon, with pia mater between.

Fig. 300.

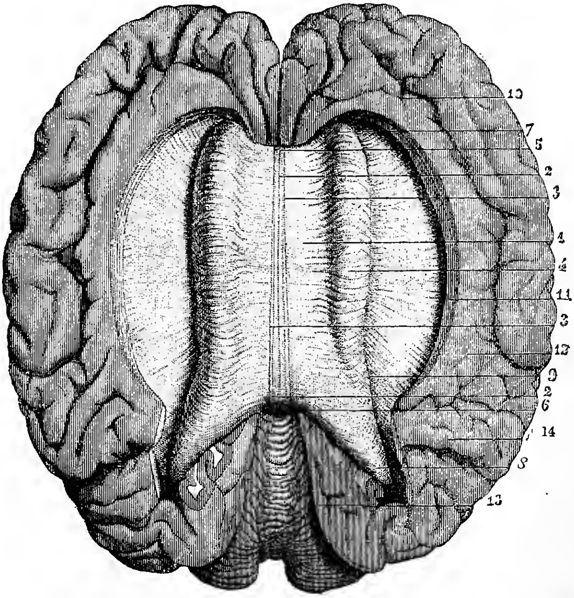


Fig. 300. — View of the corpus callosum from above (from Sappey after Foville). ½

The upper surface of the corpus callosum has been fully exposed by separating the cerebral hemispheres and throwing them to the side ; the gyrus fornicatus has been partly detached, and the transverse fibres of the corpus callosum traced for some distance into the cerebral medullary substance.

1, the upper surface of the corpus callosum ; 2, median furrow or raphe ; 3, longitudinal striæ bounding the furrow ; 4, swelling formed by the transverse bands as they pass into the cerebrum, arching over the side of the lateral ventricle ; 5, anterior extremity or knee of the corpus callosum ; 6, posterior extremity ; 7, anterior, and 8, posterior fibres proceeding from the corpus callosum into the frontal and occipital lobes respectively ; 9, margin of the swelling ; 10, anterior part of the gyrus fornicatus ; 11, fissure between the corpus callosum and this convolution opened out ; outside 12, is the termination of the calloso-marginal fissure, and before 13 is the parieto-occipital fissure; 13, upper surface of the cerebellum

Although it has a few longitudinal white fibres on its surface, the corpus callosum consists almost entirely of fibres having a transverse course, and spreading on each side in a radiating manner into the substance of the hemispheres. The greater thickness of the corpus callosum at its anterior and posterior extremities than in the intervening part is due to the increased aggregation of the fibres in the two former situations, and the greater thickness of the posterior extremity is attributable to the mass of the cerebral hemisphere which is behind the corpus callosum being larger than that in front.

The fibres are arranged in flattened bundles with the long axes of the bundles vertical but becoming horizontal at the ends. In their passage into the parietal lobes and into the posterior part of the frontal lobe their direction is nearly transverse, but from the genu they curve round into the anterior part of the frontal lobe, and from the posterior end or splenium they arch round the posterior and inferior cornua of the lateral ventricle, forming the upper and outer wall of those parts of the cavity, into the temporo-sphenoidal and the lower part of the occipital lobes. Lastly, from the under part of the splenium fibres pass with a bold sweep (forceps major) into the posterior and superior parts of the occipital lobes.

Ventricles of the cerebral hemispheres, lateral ventricles, or *ventriculi tricornes.*—By making a longitudinal cut through the corpus callosum at a short distance on each side of the middle line, and about midway between the two ends of the hemispheres, an opening is made into the right and left *lateral ventricles* (ventricles of the cerebral hemispheres).

Each lateral ventricle is connected by the cleft-like foramen of Monro with the anterior part of the third ventricle. In front of this communication the ventricle passes with a slight curve outwards and downwards into the frontal lobe of the hemisphere to form the *anterior cornu* (fig. 301, *g*), behind, the cavity extends backwards, with a slight curve outwards, as the *body of the ventricle* beneath the lateral part of the corpus callosum, and reaching as far back as the splenium of the latter. Here it bifurcates into a shorter *posterior cornu* (*h*), curving inwards and backwards into the occipital lobe, and a longer *inferior or descending cornu* (*q*), curving downwards and forwards to about an inch from the apex of the temporo-sphenoidal lobe. The whole cavity has therefore a general arched form, well shown in casts of the interior, the convexity of the arch being directed backwards, outwards and downwards, with an anterior and a posterior prolongation, this form having been assumed with the successive development of the lobes of the hemisphere around the first-formed central lobe.

The *body* of each lateral ventricle is roofed by the corpus callosum and its lateral extension, and is separated from its fellow by a hollow vertical partition, the *septum lucidum,* which extends between the corpus callosum and the fornix. In the floor of the ventricle there are seen in succession from the inner side and behind, (1) part of the *fornix,* a thin longitudinal layer of white substance, broader behind than in front (fig. 301, *f*) : (2) the *choroid plexus of the lateral ventricle* (fig. 301, *c*), a red vascular fringe, which is covered by epithelium continuous with that lining the ventricle, and projecting from below the fornix, forms the border of the velum interpositum : (3) part of the *optic thalamus,* appearing from beneath the choroid plexus (fig. 301, *l*) : (4) a narrow flat band, the *tænia semicircularis* or *stria terminalis* (*s*), which separates the optic thalamus from : (5) an elongated pyriform eminence of grey matter which extends into the anterior and inferior cornua, and is known as the *nucleus caudatus of the corpus striatum* (*k*).

The *anterior cornu* (fig. 301, *g*) is the blind anterior extremity of the ventricle, projecting a little way into the white substance of the frontal lobe. It is covered by the corpus callosum, and turns forwards and outwards round the enlarged anterior extremity of the nucleus caudatus, decending as it proceeds, and bounded below and externally by that body, in front by the reflected part of the corpus callosum, and mesially by the septum lucidum.

Fig. 301.

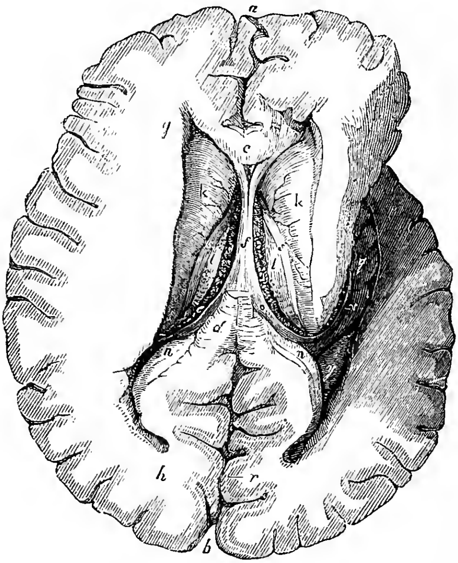


Fig. 301.—The lateral ventricles opened by removal of the middle part of the corpus callosum, and the descending cornu exposed on the right side. $\frac{1}{2}$

a, *b*, anterior and posterior parts of the great longitudinal fissure; *c*, section of the anterior part of the corpus callosum; *d*, posterior part of the same; *e*, the left choroid plexus; *f*, the fornix; *g*, the anterior; *h*, the posterior, and *q*, the descending cornu of the lateral ventricle; *k*, *k*, corpora striata; *l*, *l*, optic thalami; *n*, *n*, right and left hippocampus minor; *o*, posterior pillar of the fornix; *v*, the fimbria into which it passes; *q*, on the cornu ammonis or hippocampus major; *h*, on the medullary substance of the cerebral hemisphere; *r*, part of the grey cortical substance showing the white stria of Vicq-d'Azyr; *s*, tænia semicircularis; *y*, eminentia collateralis.

The *inferior* or *descending cornu* (*q*) turns round the back part of the optic thalamus, which is separated from its cavity by the choroid plexus with its epithelial covering. At its commencement it is directed backwards and outwards; then, passing downwards with a sweep, it curves forwards, and at its extremity has a marked inclination inwards. Its roof is formed by the fibres of the corpus callosum which are arching over it to pass to the temporo-sphenoidal lobe, and into it is prolonged a continuation of the tænia semicircularis and the posterior tapering part of the nucleus caudatus, already seen in the body of the ventricle. Near the end of the cornu a considerable prominence, the *amygdaloid tubercle*, is seen in the roof, and forms also the terminal boundary of the cornu. The principal object upon its floor is the *hippocampus major* (*cornu ammonis*), a large white eminence extending the whole length of the cornu (fig. 302, 5′, 6′). This eminence becomes enlarged towards its anterior and lower extremity, and is indented or notched on its edge, so as to present some resemblance to the paw of an animal (pes hippocampi). The white fibres of its surface form only a thin layer, and beneath them is grey matter continuous with that of the surface of the hemisphere, this eminence within the ventricle corresponding to the depres-

sion of the hippocampal fissure on the outside. Along the concave mesial edge of the eminence the white superficial layer (fig. 298, *a*) is thickened to form a narrow white band named *fimbria* or *tænia hippocampi* (fig. 302, 6), which is prolonged from the posterior pillar of the fornix; mesial to and above the fimbria is a part of the choroid plexus, covered next the cavity by epithelium prolonged from that lining the cavity. If the pia mater with the choroid plexus be pulled away, the epithelium covering the latter is removed with it, and the cornu is made to communicate with the surface of the brain along the whole length of its inner side (inferior fissure of the cerebrum).

The grey matter of the hippocampus major is continuous externally and below with that of the uncinate convolution and internally with the fascia dentata, which forms, as shown in figure 298, a free edge to the superficial grey matter of the hemisphere, the corresponding edge of the white matter being formed by the fimbria. At the end of the cornu the hippocampus is continuous with the uncus.

Fig. 302.

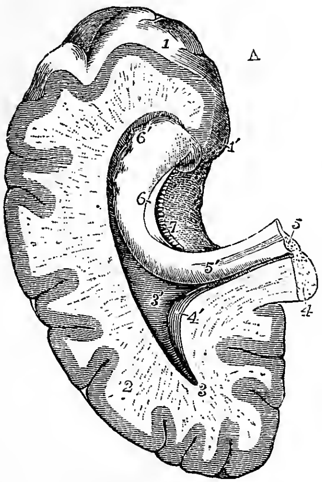


Fig. 302.—Lower and back part of the cerebrum of the left side, showing the posterior and descending cornua of the lateral ventricle opened (altered from Hirschfeld and Leveillé). $\frac{1}{2}$

1, Apex of temporo-sphenoidal lobe; 1′, uncinate convolution; 2, cut surface of the cerebral hemisphere; 3, point of the posterior cornu of the lateral ventricle; 3′, eminentia collateralis; 4, cut surface of the lower and back part of the corpus callosum divided near the middle; 4′, placed on the extension of the corpus callosum into the cerebral hemisphere, points by a line to the hippocampus minor in the posterior cornu; 5, cut edge of the posterior pillar of the fornix passing down at 5′, into the hippocampus major and fimbria; 6, placed on the hippocampus major points to the fimbria; 6′, pes hippocampi; 7, fascia dentata.

The *posterior cornu* (fig. 301, *h*) projects backwards into the substance of the posterior lobe. At its extremity it is pointed, and directed inwards. Its outer wall is formed, like that of the descending cornu, of the arching fibres passing from the corpus callosum to the temporo-sphenoidal lobe and to the lower part of the occipital lobe. The floor is formed by the medullary substance of the occipital lobe, covered, of course, as is the case with the inner surface of the ventricle everywhere, by ependyma lined with epithelium. On the inner wall is a curved and pointed longitudinal eminence, named *hippocampus minor*, *ergot*, or *calcar avis*, and above this is another longitudinal eminence (*bulb of the posterior cornu*), caused by the bundle of fibres which form the forceps major curving round from the splenium of the corpus callosum to enter the occipital lobe. At the junction of the posterior with the descending cornu, between the hippocampus major and minor, is a smooth eminence, named *eminentia collateralis*, or *pes accessorius*, which may extend some way down the descending cornu behind the great hippocampus.

The calcar avis or hippocampus minor is the convex side of the fold of

cortical substance which forms the calcarine sulcus, and in like manner the eminentia collateralis corresponds with the collateral sulcus.

The hippocampus minor is not peculiar to the human brain as was at one time thought, but is found in the brains of quadrumana. In the human subject the posterior cornu varies greatly in size, and the hippocampus minor is still more variable in its development, being sometimes scarcely to be recognised, and at others proportionally large. It is usually most developed where the posterior cornu is longest; but the length of the posterior cornu, and prominence of the hippocampus minor, are by no means in proportion to the dimensions of the hemisphere, but rather seem to be associated with thinness of both the medullary and the cortical substance.

The posterior cornu is curved round the internal parieto-occipital fissure, which may thus be regarded as causing a projection in the wall of the ventricle.

The **septum lucidum** is a thin double partition, placed between the two lateral ventricles. It is double, being composed of two distinct laminæ, having an interval between them, which contains fluid. This interval is the *fifth ventricle*, *ventricle of the septum*, or *Sylvian ventricle* (fig. 301, between *c* and *f*). It extends vertically between the corpus callosum above and in front, and the anterior part of the fornix below and behind (fig. 258) ; and as the latter gradually sinks down from the corpus callosum, the septum with its contained cavity is deep before and narrow behind, in form somewhat resembling an obovate leaf. Posteriorly it is bounded by the pillars of the fornix (fig. 307) and by the lamina cinerea.

The laminæ of the septum are formed of a part of the median wall of the hemispheres which has remained free, while the surrounding parts have become united by the development of the corpus callosum above and in front and the fornix below and behind. The ventricle of the septum was therefore originally a part of the great longitudinal fissure, and has no connection with the internal ventricular cavity of the brain. Accordingly we find that it is not lined by epithelium, but each lamina consists of a thin layer of grey matter next the cavity, and homologous with the grey matter of the cerebral cortex, and a thicker layer of white matter continuous below on either side with the general white matter of the hemisphere. Externally, next the lateral ventricle, is a layer of ependyma, and covering this the epithelium which lines the lateral ventricle.

The **fornix** (fig. 301, *f*) is an arched longitudinal white commissure, the margin of which is seen in the floor of the lateral ventricle. It consists of two lateral halves, which are separated from each other in front and behind, but in the intermediate part are joined together in the mesial plane. The two parts in front form the *anterior pillars*, or *columns*, of the fornix; the middle conjoined part is named the *body;* and the hind parts, which are again separated from each other, form the *posterior pillars* or *crura*.

The *body* of the fornix is triangular in shape, being broad and flattened behind, where it is connected with the under surface of the corpus callosum, and narrower in front, where it is connected to the septum lucidum. Its lateral edges are free and are in contact with the choroid plexuses of the lateral ventricles, and its under surface rests upon the velum interpositum, which separates it from the optic thalami and the third ventricle (see fig. 291 on p. 325).

The *anterior pillars* or *columns* of the fornix (fig. 305, *Cf*), cylindrical in form, can be traced downwards, slightly separated from each other, through the grey matter on the sides of the third ventricle, in front of the

foramina of Monro, of which they form the anterior boundaries, curving backwards to the corpora albicantia. There each column turns upon itself, making a twisted loop which forms the white portion of the corpus albicans, and from this it can be traced (as the bundle of Vicq d'Azyr), upwards into the anterior nucleus of the optic thalamus (fig. 303). Each pillar is connected near the foramen of Monro with the peduncle of the pineal gland, and with the tænia semicircularis, and it also receives fibres from the septum lucidum.

According to Gudden and Forel the fibres of the anterior pillars take origin in the grey matter of the corpora albicantia, and are not directly continuous, as in dissected preparations they seem to be, with the bundle of Vicq d'Azyr.

Fig. 303.

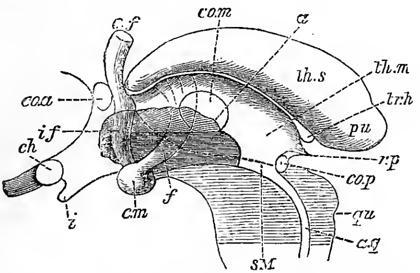


Fig. 303.—Sketch showing the origin and connections of the anterior pillars of the fornix (Schwalbe).

A median section has been made through the third ventricle, and the superficial grey matter removed at its anterior and lower part. *th.s*, upper part of the thalamus; *th.m*, its mesial surface: between the two is the medullary stria, leading from the pineal gland and trigonum habenulæ, *tr.h*, to the anterior pillar of the fornix, *c.f*; *f*, bundle of Vicq-d'Azyr; *c.m*, corpus mammillare; *i.f*, fibres of the inferior peduncle of the thalamus diverging in its substance; *co.a*, anterior commissure; *co.m*, middle commissure; *ch*, chiasma; *i*, infundibulum; *r.p*, stalk of pineal body; *qu*, corpora quadrigemina; *aq.*, aqueduct.

The *posterior pillars* or *crura* of the fornix (fig. 301, *o*) are the diverging posterior prolongations of the two flat lateral bands composing the body. At first they adhere to the under surface of the corpus callosum, then, curving outwards and downwards over the pulvinar of the optic thalamus, each crus enters the descending cornu of the lateral ventricle, where part of its fibres are distributed on the surface of the great hippocampus and the remainder are prolonged as the narrow band of white matter known as the *tænia hippocampi* or *fimbria* (fig. 302, 6), the relation of which to the fascia dentata and hippocampus has been already alluded to (see p. 346).

On examining the under surface of the fornix and corpus callosum, there is seen posteriorly the thickened border or splenium of the latter, and in front of it the diverging halves of the fornix, between which a triangular portion of the corpus callosum appears, marked with transverse, longitudinal, and oblique lines. To this part the term *lyra* has been applied (fig. 304, 12).

The **foramen of Monro** is an interval on each side between the anterior pillar of the fornix and the anterior part of the optic thalamus. This interval leads from the third ventricle to the lateral ventricle. The openings of opposite sides, passing downwards and backwards, meet in the middle line below, and thus is produced a passage, single below, but dividing into two branches above, somewhat like the letter Y, and forming a communication between the third ventricle and both lateral ventricles. This passage is named the *foramen commune anterius.*

The **transverse fissure of the cerebrum** is the name given to the cleft-like opening which is made into the ventricles when the choroid plexuses of the pia mater, which invaginate the thin epithelial wall of the ventricles, are pulled away, carrying with them the epithelium which is reflected over them from that lining the ventricle. Its extent may be made manifest after the lateral ventricles have been opened, by completely dividing the fornix and corpus callosum in the middle line, and raising the divided parts from the undisturbed velum interpositum below. It will then be found that the posterior and middle portions of the brain, including the hippocampus major and fimbria, may, by rupture of the thin epithelium which is prolonged from the fimbria to the choroid plexus, be separated from the subjacent anterior parts. The transverse fissure which is thus artificially produced extends from the extremity of the descending cornu on one side, over the optic thalami, third ventricle, and mesencephalon, to the extremity of the descending cornu of the other side. It is bounded above by the corpus callosum and fornix in the middle, and on each side by a free margin of the hemisphere formed by the fascia dentata and fimbria: inferiorly it is bounded near the middle line by the corpora quadrigemina, and on each side by the posterior part of the optic thalamus.

The **velum interpositum** or **tela choroidea** (fig. 291, *v.i.*, fig. 304) is a prolongation of the pia mater over the third ventricle and optic thalami; and its more highly vascular free borders, projecting into the

Fig. 304.

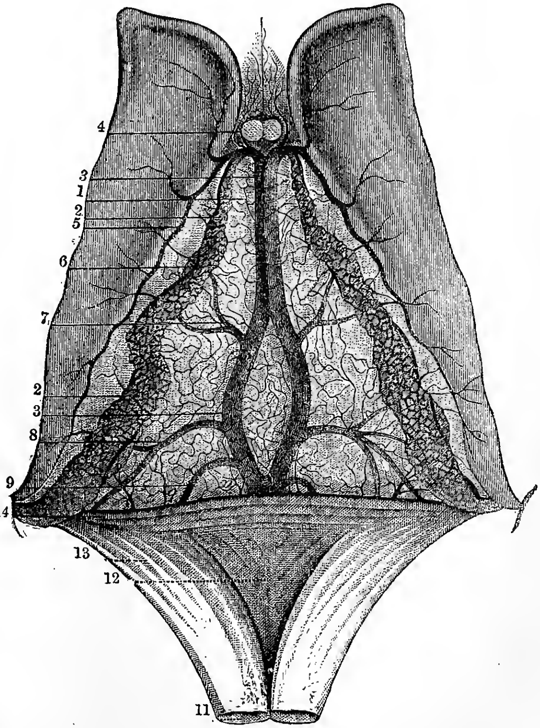


Fig. 304.—View of the upper surface of the velum interpositum, choroid plexuses, and corpora striata (from Sappey after Vicq-d'Azyr). $\frac{3}{2}$

1, fore part of the tela choroidea or velum interpositum; 2, choroid plexus; 3, left vein of Galen partly covered by the right; 4, small veins from the front of the corpus callosum and the septum lucidum; 5, veins from the corpus striatum; 6, convoluted marginal vein of the choroid plexus; 7, vein rising from the thalamus opticus and corpus striatum; 8, vein proceeding from the inferior cornu and hippocampus major; 9, one from the posterior cornu; 10, anterior pillars of the fornix divided in front of the foramen of Monro; 11, fornix divided near its middle and turned backwards; 12, lyra; 13, the posterior pillar of the fornix; 14, the splenium of the corpus callosum.

lateral ventricles, form the choroid plexuses of those ventricles. It nearly corresponds in extent with the fornix, which rests upon its upper surface.

The *choroid plexuses of the lateral ventricles* (fig. 301, *c*; fig. 304, 2, 2) extend from the foramen of Monro, to the point of each descending

Fig. 305.

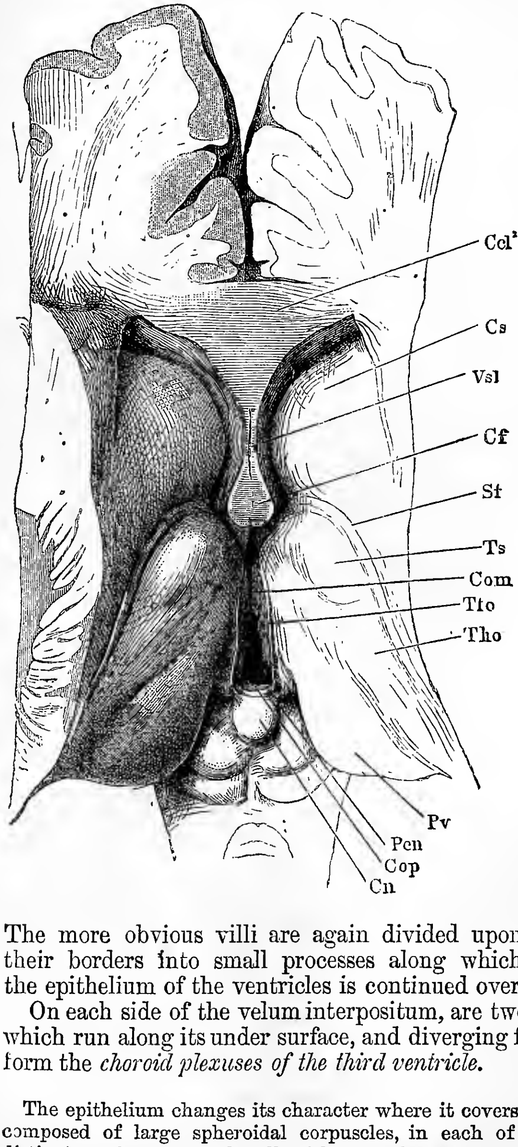


Fig. 305. — View from above of the third ventricle and a part of the lateral ventricles (Henle).

The brain has been sliced horizontally immediately below the corpus callosum, and the fornix and velum interpositum have been removed.

Tho, thalamus opticus; *Ts*, its anterior tubercle; *Pv*, pulvinar; *Com*, middle commissure stretching between the two optic thalami across the middle of the third ventricle; *Cf*, columns of the fornix; *Cn*, pineal gland projecting downwards and backwards between the superior corpora quadrigemina; *Sf*, stria terminalis; *Cs*, nucleus caudatus of the corpus striatum; *Vsl*, ventricle of the septum lucidum; *Ccl*², section of the genu of the corpus callosum; *Pen*, commencement of the pineal stria or peduncle, *Tfo*; *Cop*, posterior commissure.

cornu. Like the choroid plexuses of the 4th and 3rd ventricles these also are highly vascular and their ventricular surface is beset with villus-like projections. The more obvious villi are again divided upon their surfaces and at their borders into small processes along which fine vessels run, and the epithelium of the ventricles is continued over their surface.

On each side of the velum interpositum, are two slight vascular fringes which run along its under surface, and diverging from each other behind, form the *choroid plexuses of the third ventricle.*

The epithelium changes its character where it covers the plexuses. It is there composed of large spheroidal corpuscles, in each of which is seen, besides a distinct nucleus, several yellowish granules, and one or more dark round oil-

drops. According to Henle each of these cells is provided with short acuminate processes.

The choroid artery enters the velum interpositum at the lower end of the descending cornu ; and other arteries enter from behind, beneath the corpus callosum. The greater number of the veins terminate in two principal vessels named the veins of Galen, which run backwards on the velum interpositum, and passing out beneath the corpus callosum pour their blood into the straight sinus, having generally first united into a single trunk.

The **corpora striata** (*ganglia of the cerebral hemispheres*), situated in front and to the outer side of the optic thalami, are two large ovoid

Fig. 306.

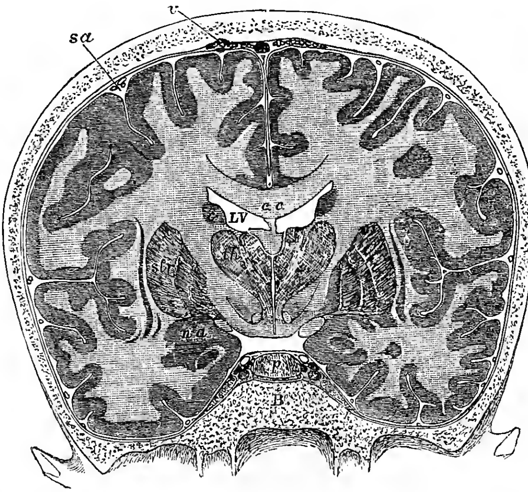


Fig. 306. — Transverse section through the brain and skull made whilst frozen (Key and Retzius). $\frac{1}{2}$

c, c, corpus callosum ; below its middle part the septum lucidum, and below that again the fornix ; *L V,* lateral ventricle ; *th,* thalamus; between the two thalami the third ventricle is seen ; below the thalamus is the substantia innominata ; *str*, lenticular nucleus of the corpus striatum ; *c,* caudate nucleus of the same ; between *th* and *str* is the internal capsule ; outside *str* is the thin grey band of the claustrum, and outside this again the island of Reil at the bottom of the Sylvian fissure ; *n, a,* nucleus amygdalæ ; immediately within this is the optic tract seen in section ; *p,* pituitary body ; *B,* body of the sphenoid bone ; *sa,* subarachnoid space ; *v,* villi of the arachnoid.

masses of grey matter, the greater part of each of which is embedded in the white substance of the hemisphere (extraventricular portion), whilst a part becomes visible in the body and anterior cornu of the lateral ventricle (intraventricular portion).

The *intraventricular portion of the corpus striatum* (**nucleus caudatus**) (fig. 305, *Cs*) is of pyriform shape, its larger end being turned forwards and appearing in the floor of the anterior cornu, and at one part reaching the outer margin of the ventricle. Its narrow end is prolonged backwards and outwards along the body of the ventricle and into the roof of the descending cornu, passing nearly to the extremity of the latter. On cutting into it, there may be seen at some depth from the surface bundles of white fibres which are prolonged through it from the inner capsule, and give it the streaked appearance from which the name corpus striatum has been derived.

The *extraventricular portion of the corpus striatum* (**nucleus lenticu-

laris) is separated from the intraventricular part by a layer of white substance (*internal capsule*), but this is bridged across in front by bands of grey matter. The lenticular nucleus is only seen on section of the hemisphere. Its horizontal section (fig. 307, *n.l*) somewhat resembles

Fig. 307.

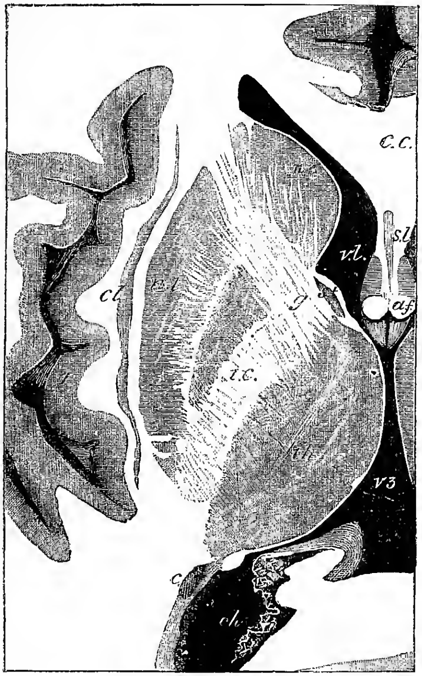


Fig. 307. — Horizontal section through part of the cerebral hemisphere (E.A.S., after a preparation by Mr. Shattock). Natural size.

The section is viewed from below; *v. l*, lateral ventricle, anterior cornu; *c. c*, corpus callosum; *s. l*, septum lucidum; *a. f*, anterior pillars of the fornix; *v* 3, third ventricle; *th*, thalamus opticus; *st*, stria terminalis; *n. c*, nucleus caudatus, and *n. l*, nucleus lenticularis of the corpus striatum; *i. c*, internal capsule; *g*, its angle or genu; *c*, tail of the nucleus caudatus appearing in the descending cornu of the lateral ventricle; *cl*, claustrum; *I*, island of Reil.

that of a biconvex lens, being wider in the centre than at either end. The antero-posterior diameter corresponds closely with that of the island of Reil, and the greatest width is opposite the anterior edge of the optic thalamus. On a transverse vertical section through the middle (fig. 306, *str*), this nucleus appears triangular, and two white lines (medullary laminæ), parallel to the outer side, divide it into three zones, of which the outer is the largest and of a dark reddish colour marked with fine white striæ, whilst the inner two are more yellowish in tint. On its outer side is a grey lamina, termed the *claustrum*, which is separated from the lenticular nucleus by a stratum of white substance named the *external capsule*. The inner capsule, or radiation of the crusta, separates it in the greater part of its extent from the caudate nucleus and thalamus, but anteriorly the two nuclei of the corpus striatum are united at their bases, and posteriorly the lenticular nucleus is continuous below with the superficial grey matter forming the anterior perforated lamina, with which the claustrum is also connected.

The **claustrum** (figs. 291, 307, *cl*) is a thin lamina of grey matter which is smooth next the outer capsule but ridged and furrowed externally, the ridges and furrows corresponding to the gyri and sulci of the central lobe, with the white substance of which the claustrum is in immediate relation. According to Meynert the claustrum is to be looked upon as a separated part of the grey cortex of the central lobe.

Along the inner border of the nucleus caudatus, in a depression between it and the optic thalamus, is seen a narrow whitish semitransparent band already noticed in the description of the ventricle, named **tænia semicir-**

cularis or **stria terminalis** (fig. 305, *Sf*), which is continued backwards into the white substance of the roof of the descending cornu. In front where it is largest it reaches the corresponding anterior pillar of the fornix, with which it comes into connection; at its other end it enters the nucleus amygdalæ in the inferior cornu.

The **nucleus amygdalæ** is a rounded mass of yellowish grey matter, continuous with the superficial grey matter of the apex of the temporo-sphenoidal lobe, forming a projection at the end of the descending cornu of the lateral ventricle. It is situated below the anterior part of the lenticular nucleus (fig. 306, *n.a*).

The **anterior commissure** appears in the anterior part of the third ventricle as a round bundle of white fibres, immediately in front of the anterior pillars of the fornix, and crossing between the corpora striata; its fibres extend laterally below the lenticular nuclei of the corpora striata, and then pass outwards and backwards in a curved course as a somewhat twisted longitudinal bundle which spreads out in the central lobe of the hemisphere, and is traceable to the medullary substance of the temporo-sphenoidal lobe above the descending cornu of the lateral ventricle and eventually to the nucleus amygdalæ (Ferrier).

In animals in which the olfactory lobe is well developed the anterior fibres of this commissure appear to be connected with the base of that lobe, and it is thought that in this way a communication is established between the temporo-sphenoidal lobe (and nucleus amygdalæ) of the one side and the olfactory lobe and nerves of the other side.

The anterior commissure is the first transverse commissure of the cerebrum to be developed in the embryo; it is also the most constant in the animal series.

MINUTE STRUCTURE OF THE GANGLIA OF THE CEREBRAL HEMISPHERES.

Nucleus caudatus.—Where it lies in the lateral ventricle the nucleus caudatus is covered by a layer of ependyma and over this by the ciliated ventricular epithelium. The ganglion is itself composed of a reddish grey substance like that of the outer zone of the lenticular nucleus. On the deeper side, that turned towards the inner capsule, the nucleus receives from this, as before mentioned, a number of bundles of medullated fibres. According to the account given by Meynert, the bundles pass in both directions, some serving to connect the ganglion with the peduncle of the cerebrum, others to connect it with the cortex cerebri. On the other hand, according to Wernicke it is doubtful if any of them pass to the white matter of the hemispheres, nor do they come from the crusta directly, but only after traversing the medullary laminæ of the lenticular nucleus.

The nerve-cells of the nucleus caudatus are multipolar, and both moderately large and small. In addition, peculiar spheroidal cells containing two or more nuclei are described by Henle. The connection of the cells with nerve-fibres, although probably existing, has not hitherto been demonstrated.

Nucleus lenticularis.—All three zones of the nucleus are pervaded by bundles of white fibres, but they are most conspicuous in the outer zone. The grey matter between the fibres contains many cells with yellow pigment in them. Fibres pass directly into the inner zone from the adjacent part of the inner capsule (*i. e.* from the peduncle of the cerebrum), while others from the mesial part of the peduncle, passing through the substantia innominata below the optic thalamus, curve outwards below the lenticular nucleus as a distinct bundle (ansa lenticularis) and entering its medullary laminæ are distributed in the middle and outer zones. According to Meynert if these fibres are traced downwards in the peduncle they are soon found to cross to the other side below the third ventricle and pass to the nuclei of the third and fourth nerves.

Other fibres connect the caudate with the lenticular nucleus, and others pass

from this nucleus into the corona radiata or white substance of the hemispheres and thence to the cortex.

The outer capsule is formed of fibres which are not directly connected with the lenticular nucleus but are derived partly from the anterior commissure, and in part from a portion of the ansa lenticularis.

In the **claustrum** the cells are for the most part small and spindle-shaped, and arranged parallel with the surface, resembling those which are met with in the deepest layer of the grey cortex of the hemispheres. Most of the cells contain yellow pigment.

INTIMATE STRUCTURE OF THE CEREBRAL HEMISPHERES.

The cerebral hemispheres, like the rest of the encephalon, are composed of white and grey substance, the white pervading nearly the whole of the middle of each hemisphere, where it forms what is known as the *medullary centre*, and extending into the convolutions; the grey forming a covering of some thickness over the whole surface of the convolutions (*cortex*), and occurring also at the base of the hemisphere in the form of the ganglia which have just been described.

THE WHITE MATTER consists of medullated fibres, varying in size in different parts, but in general still smaller than those of the cord and medulla. They are arranged in flattened bundles separated by neuroglia; the bundles have a somewhat rod-like appearance in transverse section.

The general direction which the fibres follow is best seen in a brain that has been hardened by immersion in alcohol or some other medium, although in an ordinary dissection of such hardened brains with the scalpel, we do not then trace the single fibres, but only the smaller bundles and lamellæ which they form by their aggregation. It must also be admitted that where they intimately decussate, the tearing of fibres across is liable to be mistaken for the separation of sets of fibres one from the other; it is necessary to correct such errors by the examination of sections under the microscope.

The fibres of the medullary centre, though forming many different groups, may be referred to three principal systems, according to the general course which they take, viz.:—1. *Ascending* or *peduncular fibres*, which pass from the isthmus encephali to the hemispheres. These fibres increase in number as they ascend through the isthmus, and still further in passing the optic thalami and corpora striata, beyond which they spread in all directions into the hemispheres. 2. *Transverse* or *commissural* fibres, which connect the two hemispheres together. 3. *Longitudinal* or *collateral* fibres (the association-fibres of Meynert), which, keeping on the same side of the middle line, connect near or distant parts of the same hemisphere.

1. The **peduncular fibres** in each hemisphere are derived in part directly from the fibres of the crusta, in part from the tegmentum, probably indirectly through the optic thalamus; and according to most observers they are reinforced as they pass the corpus striatum by fibres derived from the nuclei of that body.

a. Those fibres which are derived directly from the crusta pass between the optic thalamus and nucleus caudatus and the nucleus lenticularis in the inner capsule, probably giving off fibres from this to those ganglia, and on the other hand being here joined by fibres which issue from them. Beyond the inner capsule the fibres diverge into the general white matter of the hemispheres, forming part of the system of radiating fibres known from its fan-like arrangement as the *corona radiata* (Reil) or *fibrous cone*

(Mayo), the latter term being derived from the way in which the assemblage of radiating fibres is curved round in the form of an incomplete hollow cone as it emerges from below the nucleus caudatus, which follows the curve of the lateral ventricle.

Although it is probable that many of the fibres of the crusta pass directly into the medullary centre and through this to the grey cortex, without entering the basal ganglia of the hemispheres, this has only been definitely ascertained for one or two of the tracts of fibres which run in the crusta. The best known of these is the *pyramidal tract*, which, according to the observations of Charcot, Ferrier, and Flechsig, is traceable through a part of the inner capsule (opposite the middle of the thalamus) and corona radiata to the grey cortex of the ascending frontal and ascending parietal convolutions and the parts in the neighbourhood of these. This is of interest in connection with the fact that physiological experiment indicates the grey matter of these particular convolutions as especially concerned in governing the action of the chief groups of muscles of the body (motor-centres of Fritsch and Hitzig, and of Ferrier).

Another group of fibres which is traceable directly to the convolutions is the so-called *direct sensory tract* which passes from the external or lateral part of the crusta into the white matter of the occipital lobe of the hemisphere.

A few of the fibres of the crusta (those nearest the inner or mesial side) do not pass into the inner capsule and corona radiata but are collected into the bundle known as *ansa lenticularis* and pass outwards underneath the thalamus into the nucleus lenticularis (see p. 353).

b. The fibres which pass towards the cerebrum in the tegmentum, are originally constituted by the longitudinal bundles of the formatio reticularis of the medulla oblongata. They are reinforced as they pass upwards by sets of fibres derived from the superior peduncle of the cerebellum, and perhaps the middle peduncle according to Meynert and Broadbent; probably also from the corpora quadrigemina, and from the nerve- and other nuclei in the parts which they traverse. They become lost for the most part in the subthalamic tegmental region and in the thalamus, but on the other hand, from the outer side of the thalamus fibres stream outwards (see p. 324), and joining the general system of the corona radiata, diverge to nearly every part of the hemisphere, but especially to the temporo-sphenoidal and occipital lobes, the parts which experiment seems to indicate as being especially concerned with the functions of the special sense-organs. Other fibres, apparently continuous with this same system, pass from the posterior part of the thalamus into the optic tract.

From the lower part of the thalamus anteriorly fibres emerge forming the bundle known as the inferior peduncle of the thalamus, and curving round below the nucleus lenticularis, pass into the white substance of the island of Reil (see p. 325).

2. The **transverse** or **commissural fibres** which connect the hemispheres together include *a. The transverse fibres of the corpus callosum* (p. 342). *b. The fibres of the anterior commissure* (p. 353).

The course of these fibres has already been described at the places indicated. The fibres of the posterior commissure (p. 321) are sometimes regarded as connecting the posterior parts of the hemispheres.

3. The **longitudinal or collateral fibres** include those of *a.* the

fornix, *b.* the *tænia semicircularis,* and *c.* the *striæ longitudinales of the corpus callosum,* already sufficiently noticed; and likewise the following:—

d. Fibres of the gyrus fornicatus; fillet of the corpus callosum (Mayo); *cingulum.*—These fibres constitute the white substance of the gyrus fornicatus, and take a longitudinal course immediately above the transverse fibres of the corpus callosum. In front they bend downwards within the gyrus to which they belong, and are connected with the anterior perforated space, being joined by certain longitudinal fibres which run along the under surface of the corpus callosum near the middle line. Behind, they turn round the back of the corpus callosum and thence descend to the point of the temporo-sphenoidal lobe, where, according to Foville, they again reach the perforated space. Offsets from these fibres pass upwards and backwards into the secondary convolutions derived from the gyrus fornicatus in the longitudinal fissure.

e. Uncinate or arcuate fasciculus.—Under this name is described a white bundle, seen on the lower aspect of the hemisphere, passing across the bottom of the Sylvian fissure, and connecting the frontal with the temporo-sphenoidal lobe. The fibres of this bundle expand at each extremity, and the more superficial of them are curved or hooked sharply between the contiguous parts of the two lobes,—from which circumstance it has derived its name.

f. Inferior longitudinal fasciculus.—This is a bundle of fibres which lies close to the outer wall of the posterior and inferior cornua of the lateral ventricle and connects the temporo-sphenoidal and occipital lobes.

g. Association-fibres.—The convolutions of the cerebrum are connected with each other by white fibres, which lie immediately beneath the cortical substance. Some of them pass across the bottom of the sulci between adjacent convolutions; whilst others, which are longer and run deeper, connect convolutions situated at a greater distance from one another.

THE GREY MATTER ON THE CONVOLUTED SURFACE of the cerebrum forms a continuous layer indistinctly divided into two or three strata, by interposed thin layers of paler substance.

In examining a section macroscopically from without inwards (fig. 308, 1), we meet with—1. A thin coating of white matter situated on the surface, which on a section appears as a faint white line, bounding the grey surface externally. This superficial white layer is not equally thick over all parts of the cortical substance, but becomes thicker as it approaches the borders of the convoluted surface; it is accordingly less conspicuous on the lateral convex aspect of the hemispheres, and more so on the convolutions situated in the longitudinal fissure which approach the white surface of the corpus callosum, and on those of the under surface of the brain. It is especially well marked on the temporo-sphenoidal lobe, near the descending cornu of the lateral ventricle, where the convoluted surface is bounded by the fimbria, and it has been there described under the name of the *reticulated white substance.* 2. Immediately beneath the white layer just described, is found a layer of grey or reddish grey matter, the colour of which, as indeed of the grey substance generally, is deeper or lighter according as its very numerous vessels contain much or little blood. 3. A layer, appearing in section as a thin whitish line (line of Vicq d'Azyr, outer line of Baillarger). 4. A second grey stratum. 5. A second thin whitish layer (inner line of Baillarger). 6. A yellowish grey layer which lies next to the central white matter of the convolution. In some convolutions, especially those bordering on the calcarine fissure, the line of Vicq d'Azyr is very distinct but the inner line of Baillarger is not visible (fig. 308, 2).

This grey substance of the convolutions contains cells and fibres

embedded in neuroglia, with numerous blood-vessels, which pass vertically inwards at the surface but in the deeper parts are more irregularly disposed.

The **cells** are of various forms and sizes, many of them with numerous processes. Some of these branching cells are irregular in form and position, but the majority are more regularly pyramidal in shape, with the apex of the pyramid turned towards the surface of the convolution. The average size of the larger pyramidal cells is $\frac{1}{1800}$th of an inch in diameter at the base, and each has a rounded nucleus having an average diameter of $\frac{1}{2500}$th of an inch. They generally contain a little yellowish pigment. The cells often appear to lie in distinct cavities in the grey matter (pericellular spaces), but it is uncertain if these are natural or

Fig. 308.

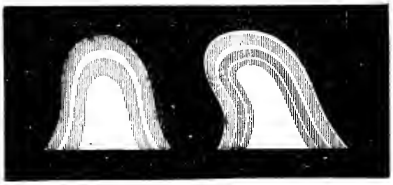


Fig. 308.—Sections of cerebral convolutions (after Baillarger).

The parts are nearly of the natural size. 1, shows the six layers ordinarily seen in the cerebral cortex when carefully examined with the naked eye; 2, the appearance of a section of a convolution from the neighbourhood of the calcarine fissure.

produced by shrinking after death. The process from the apex of each cell may be traced for some distance towards the surface of the convolution giving off one or two branches as it passes outwards. The mode of termination of these branches is unknown. Several fine branching processes pass from the angles at the base of the cell and run outwards or towards the medullary centre. Some of these processes divide and ramify, the branches forming a network of fine anastomosing fibres, while others have been traced inwards undivided, and one process at least from each cell is probably continuous with the axis-cylinder of a nerve-fibre. The undivided axis-cylinder process, according to some observers, arises from the centre of the base of the cell. The processes of these cells, as well as the body of the cell itself, possess a distinct longitudinal striation. The smaller angular corpuscles are also provided with branches which run in various directions, and probably unite into a fine network. Rounded cells, tolerably uniform in size (about $\frac{1}{2500}$th of an inch in diameter), and having no visible processes also occur.

The **fibres** radiate from the white centre of each convolution in all directions into the grey cortex, having a course for the most part perpendicular to the free surface. In passing through the grey substance they are arranged in bundles about $\frac{1}{1500}$th of an inch in diameter, and thus separate the nerve-cells into elongated groups, and give the section a columnar appearance. The direction of the fibres varies according to the part of the convolution in which they occur, whether near the summit or the base, and the radiating direction is somewhat lost in the sulci between the convolutions, where the arched fibres which connect the adjacent convolutions seem to obscure the radiating bundles. Other fibres pass in various directions through the grey substance, connecting its several layers. Gerlach describes bundles of medullated fibres at right angles to the radiating bundles, and forming with them a large-

Fig. 309.

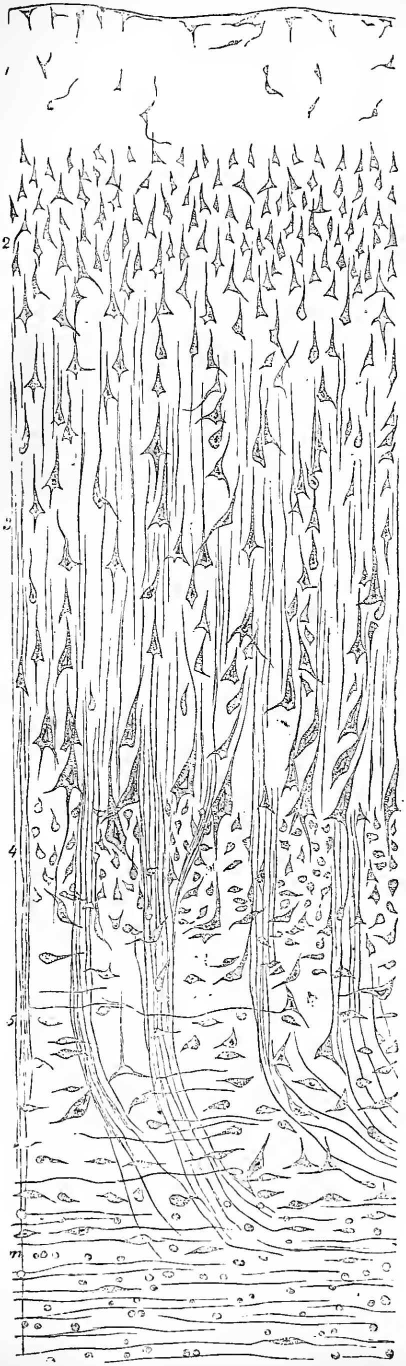


Fig. 309.—Section of cerebral convolution (Meynert).

1, Superficial layer with scattered corpuscles; 2, layer of small pyramidal corpuscles; 3, broader layer of pyramidal corpuscles, separated into columns by the radiating nerve-fibres; 4, narrow layer of small irregular corpuscles; 5, layer of fusiform and irregular cells in medullary centre.

meshed network, in the interstices of which is a still finer network, composed of the finest non-medullated nerve fibres, and formed, he believes, as in the grey substance elsewhere, by the interlacement and anastomosis of the ramifying processes from the nerve-cells.

Layers of cells in the cortex.—The form and arrangement of the cells vary at different depths of a convolution, and in this way several layers are distinguished, having more or less definite characters, but not sharply marked off from one another. Their relation to the stratification distinguishable by the naked eye is not clearly made out. The most common type is that which is seen in the convolutions of the parietal lobe. In this most observers agree with Meynert in recognising five layers as follows (fig. 309):—

1. The most external layer is narrow, and forms about $\frac{1}{10}$th of the whole thickness of the grey cortex. It is composed chiefly of neuroglia, and contains a few small cells, with fine processes, probably not of nervous character (Bevan-Lewis and H. Clarke). A few medullated nerve-fibres occur in it, forming a thin superficial white stratum immediately underneath the pia mater.

2. The next layer, of nearly the same thickness, is characterized by containing a large number of small nerve-cells, mostly pyramidal, with branching processes.

3. The third layer is of paler tint and much greater thickness. It contains pyramidal branching cells, large and small, arranged as above described, with the pointed extremities towards the surface of the convolution, and separated into groups by the bundles of radiating nerve-fibres. The inner portion of the layer, in which the cells are larger and the separation into groups more distinct, is sometimes described as a separate layer.

4. The fourth layer is narrower, and contains many small, irregularly-shaped corpuscles, round or angular, with fine processes, placed irregularly and less distinctly separated into groups.

5. The fifth layer, of greater width than the last, and blending more or less with it, is composed of fusiform and irregular cells. The fusiform corpuscles have a definite arrangement, being placed for the most part vertically at the summit of a gyrus; but in the sulci, parallel to the surface, where they correspond in direction to the arcuate fibres passing from one convolution to another; they are said to be connected with these fibres.

Beneath the last layer is the medullary centre, with which it gradually blends. The fibres of the white substance, as they radiate into the grey matter, become finer. They terminate partly in the axis-cylinder processes of the pyramidal cells, partly in two plexuses of medullated fibres which lie, the one at the base of the layer of large cells or 3rd layer, the other between this and the layer of small pyramidal cells (2nd layer). These plexuses (inner and outer white plexuses of W. Krause) are probably the cause of the whitish lines seen with the naked eye in a section of the grey cortex of a fresh brain.

In the Sylvian fissure the fusiform cells are more abundant than elsewhere, and from their number in the claustrum the fifth layer has been termed by Meynert the "claustral formation." They are also very abundant in the amygdaloid nucleus, which is indeed chiefly formed by a thickening of the deepest layer of the cerebral cortex. The cornu ammonis on the other hand is formed almost exclusively of the large pyramidal corpuscles, and the layer in which these corpuscles occur (third layer) has, in like manner, been termed the "formation of the cornu ammonis."

Differences of structure in different parts.—Considerable variety occurs in different parts of the cerebral cortex in the size and regularity of shape of the nerve-cells and in the relative thickness of the several layers. It is especially worthy of notice that in the region of the motor centres and particularly in the upper part of the ascending frontal convolution, some of the deeper pyramidal cells are very large, and are arranged in more or less defined groups or nests (Betz). From their size these deeper cells are often termed the "giant-cells" of the cerebral cortex, but by Lewis and H. Clarke they are named the "ganglionic cells," and are described as situated amongst the small cells of the fourth layer, which is therefore denominated the ganglionic layer. On the other hand, in the neighbourhood of the calcarine fissure, in the occipital lobe, large cells are very scanty, their places being for the most part taken by smaller ones. Again, in many parts a six-laminated cortex is produced by the intercalation of a layer of small angular cells between the third layer and the ganglionic layer (Lewis).* But the most remark-

* For an extended account of the structure of the cerebral cortex in man and animals the reader is referred to a paper by Bevan-Lewis and H. Clarke in the "Proceedings of the Royal Society," vol. xxvii., 1878; and to papers by Bevan-Lewis, in the "Philosophical Transactions" for 1880 and 1882, and in "Brain," and by Betz in the Med. Centralbl., 1881.

able differences of structure occur at the incurved margin of the hemisphere in the region of the cornu ammonis or hippocampus major, and in the olfactory lobe. These will now be specially considered.

Fig. 310.

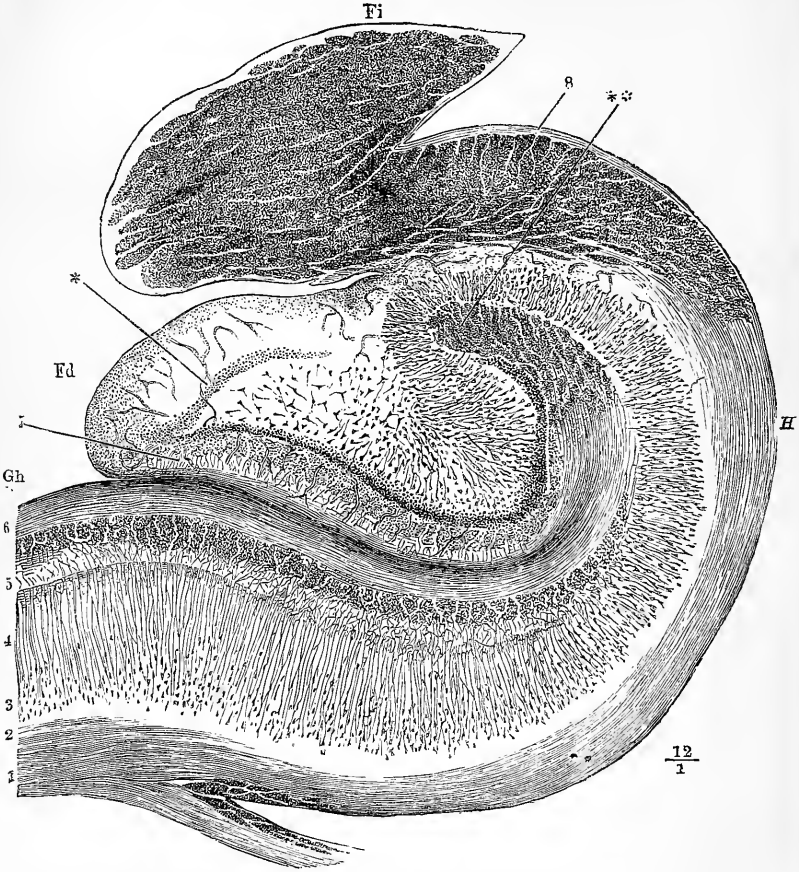


Fig. 310.—SECTION ACROSS THE HIPPOCAMPUS MAJOR, DENTATE FISSURE, DENTATE FASCIA AND FIMBRIA (after Henle).

Gh, part of the gyrus hippocampi or uncinate convolution ; *Fd,* fascia dentata or dentate convolution ; between them is the dentate fissure ; *Fi,* fimbria, composed of longitudinal fibres here cut across ; 1, 2, medullary centre of the hippocampal gyrus prolonged around the hippocampus, *H,* as the so-called alveus, into the fimbria ; 3, layer of large pyramidal cells ; 4, stratum radiatum ; 5, stratum laciniosum ; 6, superficial medullary lamina, involuted around the dentate fissure ; **, termination of this lamina, the fibres here running longitudinally ; 7, superficial neuroglia of the fascia dentata ; *, stratum granulosum.

Structure of the hippocampus major or cornu ammonis.—The hippocampus it will be remembered corresponds to the hippocampal fissure externally ; this fissure separating the uncinate convolution below from the fascia dentata above. The uncinate convolution (fig. 298, *b*) has the ordinary structure of the cerebral gyri, being composed of a superficial grey cortex and a thick white centre. The grey cortex is prolonged around the hippocampal fissure, there becoming some-

what thickened, and forming the main part of the hippocampus; the white centre is also prolonged over the projection of the hippocampus into the ventricle, but becomes very thin in this situation where it is known as the *alveus*. It is covered by the epithelium and ependyma of the ventricle.

Above the hippocampal fissure the grey matter of the hippocampus swells out into the notched lamina known as the *fascia dentata* (dentate convolution, fig. 310, *Fd*). The white matter of the alveus is in like manner prolonged over this but not so far as its free border; it becomes thickened and is continuous with the white band known as the *fimbria* (*Fi*).

The greater part of the grey matter of the hippocampus is occupied by several rows of tolerably large pyramidal cells (fig. 310, 3) with long apical processes, which lie embedded in a neuroglia-matrix, and confer upon this, especially in its outer part, a striated aspect; hence the name of *stratum radiatum* is sometimes used to distinguish this part of the layer (4). By their bases the cells rest upon the white layer or alveus, into which their axis-cylinder processes pass, but there is in some parts a thin layer of grey matter intervening.

Superficial to this *stratum of large pyramidal cells* and their processes, is a layer the neuroglia of which is characterized by its openly reticulate structure (*stratum laciniosum*, 5). The texture is more condensed both in its superficial and in its deeper parts, and in the latter are a number of small cells (*stratum granulosum*). Blood-vessels are numerous in this part, which appears to correspond with the first or superficial layer of the series met with in the typical convolution. Superficial to it again is a well-marked layer of medullated fibres continuous with the reticulated white substance of the uncinate convolution (see p. 340). It is known as the *involuted medullary lamina* (fig. 310, 6), and represents an increased development of the thin layer of white fibres which is ordinarily found next the surface of the grey matter.

In the fascia dentata the large pyramidal cells are placed in the centre and are irregularly arranged: they are surrounded by a ring of closely packed small pyramidal cells (stratum granulosum, fig. 310,*), outside which is a very broad superficial layer of neuroglia with a few scattered cells.

Minute structure of the olfactory lobe.—The peculiar structure of this part of the brain can best be understood by a reference to its mode of development. It appears to be formed as a hollow outgrowth from the vesicle of the cerebral hemisphere (afterwards the lateral ventricle), and in most of the lower animals (in which it is much more developed than in man), it exhibits even in the adult condition a central cavity (lined with ciliated epithelium), and in some this retains throughout life its connection with the lateral ventricle. The walls of the hollow outgrowth become thickened and differentiated into a central layer of neuroglia next the cavity, a well-marked intermediate layer of white substance outside this, and a peripheral layer of grey matter surrounding the whole. In man and apes the same changes occur, but the cavity becomes completely obliterated and in its stead we find nothing but the central neuroglia, which forms for the most part a tract flattened out laterally, and containing but few cells. The white or medullary substance around this appears in section in the form of a flattened ring consisting for the most part of longitudinal white fibres. In the olfactory tract the peripheral layer of grey matter is very thin and incon-

Fig. 311.

Fig. 311.—Section across the middle of the olfactory tract (Henle).

v, ventral surface; *d*, dorsal ridge. From without in are seen successively: (1) a thin superficial layer of neuroglia; (2) a (darkly shaded) layer of transversely cut medullary fibres, of very unequal thickness in different parts; (3) the central grey matter projecting up into the dorsal ridge and here and there extending to the surface and partially interrupting the medullary layer.

spicuous, so that the white substance almost everywhere shows through it, except along the dorsal ridge where there is an accumulation of the grey substance, extending into and partly interrupting the medullary ring (fig. 311, *d*). In the bulb on the other hand this dorsal accumulation of grey matter is not seen; but upon the ventral side of the flattened medullary ring (fig. 312, 1, 2, 3) in place of the thin scarcely visible layer of grey substance in the corresponding situation in the tract, several complex layers are found and form indeed the greater part of the thickness of the bulb, what was originally the central cavity being consequently now placed near the dorsal surface. These layers as seen in section occur in the following order from above down (fig. 312, 4 to 8):—

The *granule layer* (fig. 312, 4) lying next to the ventral surface of the medullary ring, is characterised by the presence of numerous small cells, like those found in the deeper or granule layer of the grey cortex of the cerebellum. The layer is not entirely composed of these cells however, for there are present in addition a number of reticulating bundles of medullated fibres concentric for the most part with the superjacent medullary ring, and serving to separate the "granules" into groups, which occupy the meshes of the plexus formed by the nerve-bundles. Some medullated fibres also pass vertically in this layer (L. Clarke).

Fig. 312.

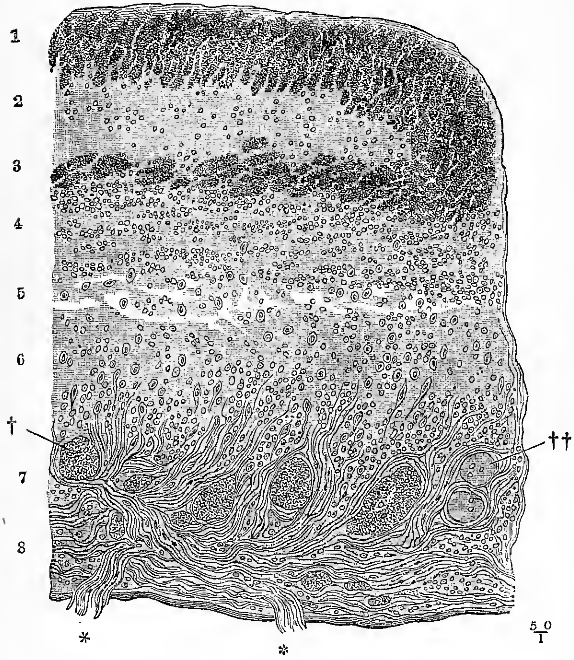


Fig. 312. — SECTION ACROSS A PART OF THE OLFACTORY BULB (Henle).

1, 3, layers of very fine transversely cut nerve-fibres, passing round into one another at the side, and forming the flattened medullary ring, enclosing the central neuroglia, 2; 4, granule-layer; 5, loose tissue with irregular spaces (? lymphatic); 6, intermediate layer; 7, layer of olfactory glomeruli, †, ††; 8, layer of olfactory nerve-fibres.

The *intermediate* or *nerve-cell layer* (6), which is partly marked-off from the granule layer by the presence of cleft-like lymphatic spaces (5), consists of grey or gelatinous substance (neuroglia) in which nerve-cells are embedded, having for the most part a pyramidal or conical shape, like those which characterize the grey matter of the cerebral convolutions. The largest of these cells lie next to the granule layer, where they form an almost continuous stratum, their bases being directed towards that layer, and their apices projecting downwards into the grey substance of their own layer. They appear to correspond to the stratum of large nerve-cells in the deeper part of the cortex of the cerebral hemispheres. Smaller cells lie scattered in the neuroglia, which is traversed also by numerous medullated fibres.

Layer of the olfactory glomeruli (7). The remarkable bodies which characterize this stratum were first described by Leydig in elasmobranchs and by

Lockhart Clarke in mammals. They appear to consist of rounded nests of small cells, probably small ganglion-cells which give origin to the fibres of the olfactory nerves. The glomeruli form an irregular layer one or two deep, and are separated from one another by bundles of non-medullated fibres which pass into the subjacent layer. Within each glomerulus, the nerve-fibres are found to form a tangled convolution amongst the cells.

Layer of olfactory nerve-fibres (8). This, the deepest layer of the bulb, consists entirely of bundles of non-medullated nerve-fibres, which become collected here into a dense plexus before sending down the branches (* *) which pass through the perforations in the cribriform plate of the ethmoid bone.

Although the whole of the olfactory tract and bulb has been generally termed by human anatomists the olfactory nerve or first pair, the facts brought to light by the study of their development, comparative anatomy, and microscopic structure clearly indicate that these parts are not homologous with the ordinary cranial and spinal nerve-roots but are in reality parts of the brain itself. It is supposed by Krause that the layer of olfactory glomeruli is homologous with the ganglion on the posterior root of a spinal nerve.

ORIGIN OF THE CRANIAL NERVES.

In describing the origin of the cranial nerves the surface attachment or superficial origin of the roots has to be distinguished from their deep origin in the collections of nerve-cells known as the nuclei of the respective nerve-roots. Most of these nuclei have been already referred to in the description of the medulla oblongata, pons and mesencephalon, but their situation and relations may be here briefly recapitulated.

The olfactory tract and bulb (fig. 313, I) form what have usually been described as the **first** or **olfactory nerve**. As already stated they are really however a part of the cerebral hemisphere, and must be regarded as forming a distinct lobe, the *lobus olfactorius*. Their structure and attachments have already been described. The fibres which pass from the olfactory bulb through the perforations in the cribriform plate of the ethmoid bone to be distributed over the upper part of the nasal mucous membrane, collectively represent the first cranial nerve.

The **second** or **optic nerves** (fig. 313, II), which are developed as hollow outgrowths of the wall of the first primary cerebral vesicles, come off on each side from the anterior part of the chiasma, and enter the optic foramina. After curving round the crura cerebri from their origin in the geniculate bodies, the posterior part of the thalami, and the anterior quadrigeminal bodies (see p. 320 and figs. 260, 261), the optic tracts enter the chiasma at its posterior and lateral angles. In the chiasma the fibres of the tract for the most part pass diagonally across to enter the optic nerve of the opposite side, but a few fibres pass directly into the optic nerve of the same side.

In addition to the fibres which enter the optic nerves there is a small band at the posterior part of the optic tract and chiasma which simply passes across uniting the two inner geniculate bodies. This is the *inferior commissure* of Gudden. A similarly arched bundle of fibres was formerly described at the anterior margin of the chiasma, as serving to unite the retinæ of the two sides, but its existence is considered doubtful by most observers, although it has recently been affirmed by Stilling.

In all the lower vertebrates, and in many mammals, the decussation of the optic tracts is complete; that is to say, all the fibres of the optic tract of the one side (with the exception of the small inferior commissure just alluded to) pass across into the optic nerve of the same side. But, in some mammals at least, including man, there are strong reasons, chiefly derived from pathological observations, for believing that a few of the fibres do not thus decussate. The diffi-

culty of tracing the course of the fibres in the chiasma is very great in consequence of the fact that they take, not a straight, but a curved course within the commissure. The fibres of the optic tract come from the anterior quadrigeminal body through its brachium; from the inner geniculate body; from the external geniculate body and the thalamus; and lastly a few are said to pass into the anterior part of the tract, where this is in contact with the tuber cinereum, from the basal optic ganglion of Meynert (see p. 327). According to Stilling a bundle of fibres passes to the optic tract from the corpus subthalamicum. and another bundle can be traced up to it from the pyramidal decussation in the medulla (Arch. f. micr. Anat. xviii, 1880).

The **third** or **oculomotor nerve** (fig. 313, III) arises from a column of large yellowish cells, on either side of the middle line, in the grey matter

Fig. 313.

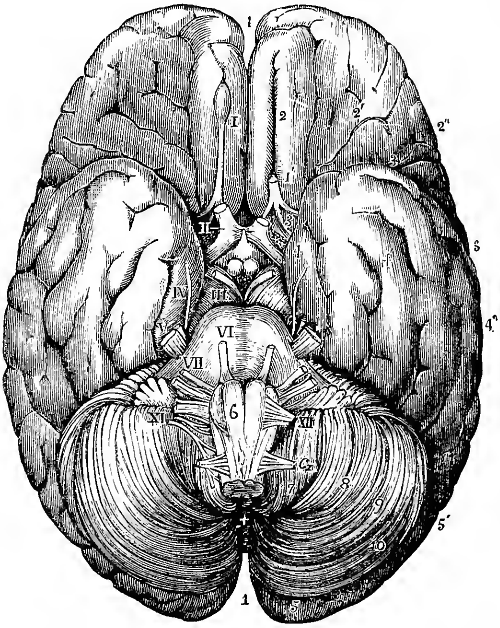


Fig. 313.—Base of the brain with the origins of the cerebral nerves (Allen Thomson). $\frac{1}{2}$

This figure is taken from an adult male brain which had been hardened in alcohol.

1, superior longitudinal fissure; 2, the olfactory tract and sulcus; 2′, orbital convolutions; 2″, inferior frontal convolution; 3, 3, 3, fissure of Sylvius; 4, 4, 4, temporo-sphenoidal lobe; 5, 5′, occipital lobe; 6, on the right anterior pyramid of the medulla oblongata above the decussation; 7, amygdaloid lobe of the cerebellum; 8, biventral lobe; 9, slender lobe; 10, posterior inferior lobe; +, the inferior vermiform process; I, olfactory bulb; I′, the tract divided on the left side; II, in the anterior perforated spot, marks the right optic nerve; the left has been cut short; III, on the right crus cerebri, denotes the third nerve; IV, the fourth nerve; V, the fifth; VI, on the pons Varolii, the sixth; VII, also on the pons Varolii, the facial with the auditory nerve on its outer side; XI, on the cerebellum below the flocculus, indicates the spinal accessory nerve; between it and the auditory are seen the glosso-pharyngeal and the vagus; XII, on the upper part of the left amygdaloid lobe, denotes the hypoglossal nerve; C^1, on the same, the suboccipital nerve.

Compare also figs. 260 and 261, pp. 283 and 285.

of the floor of the Sylvian aqueduct, in the region of the superior corpora quadrigemina (fig. 286, B) extending as far forwards as the level of the posterior commissure. Inferiorly, it is continued with scarcely any interval by the nucleus of the fourth nerve. From this column of cells the fibres pass forwards through the tegmentum and the tegmental nucleus, and partly through the substantia nigra, to emerge at the line of the oculomotor groove on the inner surface of the crus cerebri close to the pons. A small part of the root often emerges from between the fibres of the crusta, and joins the trunk of the nerve independently.

From the nucleus of the third nerve a few fibres pass towards the raphe, perhaps to join the nerve of the opposite side, perhaps, as Meynert supposes, to pass as fibræ rectæ and enter the pyramidal tract of the other side, and to be conducted along this to the cerebrum.

The **fourth** or **trochlear nerve** arises from a nucleus which lies in the region between the superior and inferior quadrigeminal

Fig. 314.

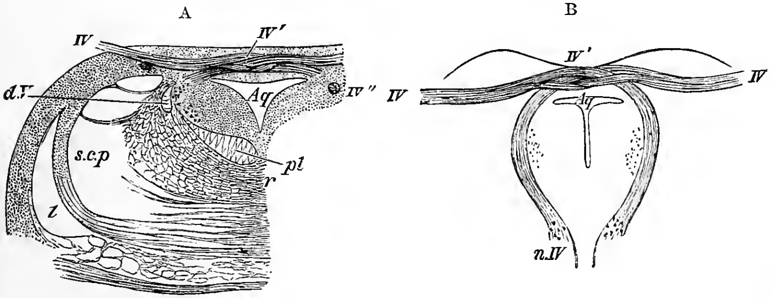


Fig. 314.—Sections through the origin of the fourth nerve (Stilling). $\frac{3}{1}$

A, transverse section at the place of emergence of the nerve-fibres. B, oblique section carried along the course of the bundles from the nucleus of origin to the place of emergence. *Aq*, Sylvian aqueduct, with its surrounding grey matter; *IV*, the nerve-bundles emerging; *IV'*, decussation of the nerves of the two sides; *IV''*, a round bundle passing downwards by the side of the aqueduct to emerge a little lower down; *n, IV*, nucleus of the fourth nerve. *l*, fillet; *s. c. p.*, superior cerebellar peduncle; *d. V.*, descending root of the fifth nerve; *pl*, posterior longitudinal bundle; *r*, raphe.

bodies immediately below that of the third nerve. The cells are larger than those of the nucleus of the third nerve. From them its fibres pass obliquely downwards and backwards, uniting to form one or more round well-marked bundles, which run in the wall of the aqueduct to reach its posterior extremity (fig. 314, *IV''*); here the fibres curve inwards and pass over the commencement of the aqueduct in the anterior medullary velum across to the opposite side, emerging from the velum close to the middle line (fig. 287, *IV.*), and passing round the crus cerebri to reach the base of the brain (fig. 313, IV.).

According to some observers the decussation of the two nerves is not complete, but some of the fibres are derived from the nucleus of the same side.

The **fifth** or **trigeminal nerve** emerges from the side of the pons Varolii, nearer to the upper than to the lower border (fig. 313, V.). It consists of two parts of unequal size, the smaller, motor, root being separated from the other by a few transverse fibres of the pons.

The **motor root** arises from a nucleus (*motor nucleus of the fifth*, fig. 273, *nv'*, fig. 316, *n* V^3), which lies just below the lateral angle of the fourth ventricle, immediately in advance of the facial nucleus, and mesial to the larger sensory nucleus of the fifth. The cells of the motor nucleus are large, ramified and pigmented. The motor root, after emerging from its nucleus, passes obliquely forwards and outwards, and is joined by fibres from the so-called *descending root of the fifth* (fig. 315 B, *n* V^4). The fibres of this arise at the side of the grey matter of the aqueduct in the region of the superior corpora quadrigemina, from some large cells which occur in the grey matter there and increasing in number as they pass downwards form a small but distinct bundle of relatively large fibres in the lower part of the mesencephalon (fig. 314, A, *d. V*). The motor root is further joined by fibres from the raphe (see fig. 273), supposed to come either from the nucleus of the other side, or from the pyramidal tract.

The **sensory root** springs for the most part from the *superior sensory nucleus of the fifth* (fig. 315, *n* V^2; fig. 273, *n v*) a collection of small nerve-cells of greater extent and less compact than the motor nucleus, on the outer side of which it lies. It receives also a considerable bundle of fibres derived from the so-called *ascending root of the fifth* (fig. 315

Fig. 315.

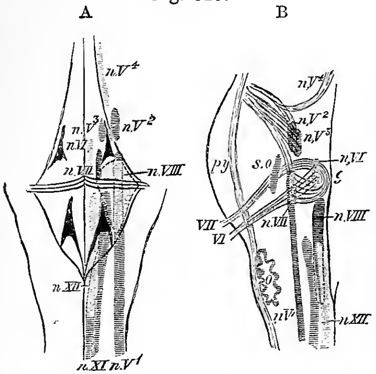


Fig. 315.—Diagrams to show the situation of the chief nerve-nuclei in the medulla and pons. Natural size. (E. A. S.)

A, from behind; B, profile view of the right half, the medulla and pons being bisected, and supposed to be transparent. The nuclei which are nearest the posterior surface in A, and the mesial plane in B are shaded more lightly; *o*, olivary nucleus; *s. o.*, superior olivary nucleus; *py*, pyramidal tract; *n* V^1, inferior nucleus and ascending root of the fifth nerve; *n* V^2, superior sensory nucleus of the fifth; *n* V^3, motor nucleus of the fifth; *n* V^4, fibres of the descending root of the fifth; *n VI*, nucleus of the sixth nerve, *VI*; *n VII*, nucleus of the facial nerve; *VII*, facial root issuing; *g*, its genu; *n VIII*, principal nucleus of the auditory nerve; *n IX*, *n X*, *n XI*, nucleus of the glossopharyngeal, vagus and spinal accessory nerves; *n XII*, nucleus of the hypoglossal.

B, *n* V^1). This is the well-marked bundle seen cut across in most sections of the medulla oblongata and pons, coursing in close contiguity with the gelatinous substance which forms the upward prolongation of the tubercle of Rolando. Its fibres are believed to arise from the nerve-cells in the gelatinous substance, which has accordingly been termed the *inferior nucleus of the fifth*. The sensory root of the fifth also receives fibres from the raphe, and others are believed to pass into it from the cerebellum.

The sensory nucleus is covered superficially by the substantia ferruginea, a collection of large deeply pigmented nerve-cells, which extends forwards in the grey matter from the superior fovea as far as the inferior corpora quadrigemina. These cells however have, so far as is known, no axis-cylinder processes, and no connection with the origin of the fifth nerve.

The **sixth** or **abducent nerve** arises from a nucleus (*nucleus of the*

sixth, fig. 315, *n. VI.;* fig. 272) which lies underneath the fasciculus teres in the floor of the fourth ventricle, a little in advance of the medullary striæ. The fibres of the nerve-root pass from the inner side of the nucleus, and curve forwards and slightly downwards through the substance of the pons to issue just below that body, and immediately above the outer border of the pyramid of the medulla.

From the nucleus of the sixth nerve a few fibres are believed to pass upwards and across the raphe to join the third nerve of the opposite side. The peculiar cases of conjugate paralysis involving the internal rectus of the one side, and external rectus of the other side, which are accompanied by atrophy of the nucleus of the sixth nerve, are thus accounted for (Duval and Laborde).

The **seventh** or **facial nerve** (portio dura of the seventh pair of Willis) takes origin in a nucleus (*nucleus of the facial*) which lies in the formatio reticularis at the same level as the nucleus of the sixth, but more deeply placed in the substance of the pons (figs. 315, 272, *n. VII*). The upper end of the nucleus comes nearly in contact with the motor nucleus of the fifth, so that the two nuclei are often described as one ; its lower end is in a line with a collection of grey matter in the medulla known as the nucleus ambiguus (fig. 268, *n.am.*). From its nucleus the fibres of the facial nerve pass backwards and inwards to the floor of the fourth ventricle (first part of the root). Here they are collected into a compact bundle, oval in section, which passes for about five millimeters upwards in the fasciculus teres, immediately beneath the ependyma of the ventricle (second part of the root), and then curves outwards over the upper end of the nucleus of the sixth to reach its outer side. From here the third or issuing part of the root makes a sharp bend (*genu*, fig. 315 B, *g*) and passes outwards and forwards, with a slight downward inclination to appear at the lower border of the pons Varolii in a line with the attachment of the fifth nerve. It emerges from the medulla oblongata, in the outer part of the depression between the olivary body and the restiform body, and is often firmly adherent, as a flattened band, to the lower edge and even for a short distance to the anterior surface of the pons. On its outer side is the auditory nerve. A separate fasciculus of the facial nerve (*pars intermedia*) is sometimes attached to both auditory and facial nerves.

As it passes the outer side of the nucleus of the sixth, the facial root appears to receive fibres from that nucleus, but it is somewhat uncertain whether this is really the case or not. Its fibres are reinforced by the axis-cylinder processes of cells which are interpolated amongst them in the first and second parts of the root (Laura), and also, perhaps, through the raphe from the nucleus of the opposite side. According to Meynert it may be connected through the raphe with the pyramidal tract of the opposite side, and in this way with the cerebrum.

The **eighth** or **auditory nerve** (portio mollis of the seventh pair of Willis). The *inner or principal nucleus of the auditory nerve* (fig. 315, *n VIII*) corresponds in extent with the prominence of the tuberculum acusticum seen in the floor of the 4th ventricle (p. 291). This extends from the lateral region of the calamus scriptorius beyond the striæ medullares into the lateral region of the upper part of the ventricle, being widest opposite the medullary striæ. The vagus nucleus is on its inner border below, but higher up it overlaps the nucleus of the glossopharyngeal and lies alongside the upper end of the nucleus of the hypoglossal. Along its outer side in the lower part is the restiform body.

From this nucleus one (*the inferior*) of the two roots of the auditory nerve arises and, inclining outwards in front of the restiform body, receives, as it appears on the surface of the medulla, a reinforcement from the fibres of the medullary striæ which have passed over the outer side of the restiform body. It may also obtain some from the restiform body itself. It is uncertain whence the fibres of the striæ medullares are derived, but it has been conjectured that they may come from the nucleus of the opposite side through the raphe.

The *outer* or *superior auditory nucleus* (nucleus of Deiters, Laura) commences at the level of the medullary striæ where it lies between the inner nucleus and the restiform body, and extends upwards from here for some distance, becoming larger above and approaching the posterior surface of the pons near the lateral angle of the fourth ventricle. Its cells are very large, whereas those of the inner nucleus are small, and, according to Laura, they send their axis-cylinder processes towards the raphe. The nucleus is traversed by longitudinal bundles which pass to or from the cerebellum, and from these bundles as well as from the outer nucleus, the *superior root* of the auditory nerve appears to arise.

Both superior and inferior roots pass obliquely outwards and unite into a single trunk which appears at the lower edge of the pons on the outer side of and close to the facial nerve. It is also united to the lower edge of the pons opposite the inner side or middle of the restiform body from which it in part emerges. Both roots contain nerve-cells interspersed amongst their fibres, and in the inferior root these cells produce a distinct pyriform swelling. The nerve-fibres of the inferior root are much smaller than those of the superior.

In addition to the two nuclei above-mentioned there is a collection of grey matter and nerve-cells lying between the superior root and the restiform body, and extending downwards into the angle between the inferior root and that body. This has received the name of *accessory auditory nucleus*. Its cells, although of small size, are peculiar in having a nucleated sheath like the cells of a ganglion. It has been supposed to give origin to the pars intermedia of the facial.

The **ninth** or **glossopharyngeal nerve** arises from a column of cells (*nucleus of the glossopharyngeal*, fig. 315, *n IX*) which is continuous behind with the nucleus of the vagus. It comes close to the surface in the inferior fovea, but in front is overlapped somewhat by the inner auditory nucleus. The fibres of the nerve pass from here outwards and forwards through the medulla to emerge by a series of five or six roots (fig. 261, *IX*), attached in a vertical line to the lateral surface of the medulla, the highest being close to the auditory nerve. The issuing fibres of the glossopharyngeal are joined by some of the fibres of the so-called solitary bundle (see below).

The **tenth** or **vagus** or **pneumogastric nerve** arises from the *vagus nucleus* (fig. 315, *n X*), a continuation of the glossopharyngeal nucleus above and of the accessory nucleus below. This in the open part of the medulla lies immediately external to the hypoglossal nucleus, and is marked on the surface by the triangular raised area which leads superiorly to the posterior fovea. The nucleus is partially divided into two parts by a round longitudinal bundle of fibres known as the *solitary* or *respiratory bundle* (fig. 268, *f. s.*). Of the two the outer (*n X'*) is the smaller and contains but few cells; the inner and deeper part (*n X*) contains a large number of cells, and from it more directly the roots of the nerve pass, reinforced by fibres from the solitary

bundle. They take much the same direction through the medulla as do those of the glossopharyngeal, many of them traversing the prolongation upwards of the gelatinous substance of Rolando; and emerge from the side of the medulla to the number of twelve or more, attached in a line which is continuous with that of the glossopharyngeal roots.

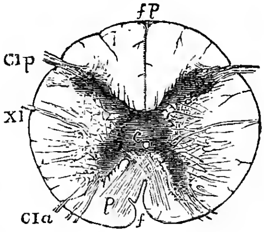
The fibres of the solitary bundle are of large size and can be traced downwards in the medulla and cord as far as the region of origin of the phrenic nerve (Krause).

The **eleventh** or **spinal accessory nerve** (fig. 315, *n XI*) arises partly in the lower part of the medulla oblongata from the continuation downwards of the vagus nucleus, partly along the whole extent of the cervical portion of the spinal cord—from the intermedio-lateral tract and adjacent part of the anterior cornu below (fig. 316), but from the reticular formation and base of the posterior cornu above. It is the former (medullary) part which joins the vagus and is distributed along with that nerve (vagal portion); the latter part (spinal portion) which originates from the cervical cord is accessory to the cervical nerves and supplies the sterno-mastoid and trapezius muscles. The part of the vagus nucleus from which the accessory takes

Fig. 316.—Section of upper end of spinal cord at the junction with the medulla oblongata. (After Lockhart Clarke.)

f, anterior; *fp*, posterior fissure; *p*, end of decussation of pyramids; *CIa*, *CIp*, anterior and posterior roots of first cervical nerve; *XI*, root of spinal accessory nerve.

Fig. 316.



origin is placed immediately behind and to the side of the central canal (fig. 267, *n XI*), where this remains closed, in a situation corresponding to the base of the posterior cornu of the spinal cord; but where the central canal opens out at the point of the calamus scriptorius, the nucleus lies just at the side of the median sulcus of the fourth ventricle. The root-fibres of the vagal portion have a course through the substance of the medulla like those of the vagus, and in every way this part of the spinal accessory resembles a separated part of the vagus. It receives a few fibres from the solitary bundle. The nerve emerges as a long series of roots the upper of which are attached to the side of the medulla in a line with the posterior roots of the spinal nerves below, and the roots of the vagus above; while the lower emerge from the lateral column of the spinal cord, which they traverse in their passage from the grey matter.

Twelfth or **hypoglossal nerve.** The *nucleus of the hypoglossal* (fig. 315, *n XII*) is a column of cells nearly three-quarters of an inch long, which in the lower part of the medulla lies antero-laterally to the central canal (fig. 267, *n XII*) in a situation corresponding to the base of the anterior cornu of the spinal cord; but soon after the canal has opened out the nucleus comes nearly to the surface of the fourth ventricle, being indicated by the narrow triangular area on either side of the median sulcus. When viewed from the surface the grey matter of the nucleus is partly concealed by transversely coursing fibres passing to the raphe. The anterior end of the column is rounded, as may be seen

in longitudinal sections, and appears connected by longitudinally coursing fibres with the nucleus of the sixth, which also lies in the fasciculus teres.

From the large multipolar cells of the nucleus most of the fibres of the hypoglossal arise and pass outwards and forwards through the substance of the medulla, to emerge by a series of fine roots at the furrow between the pyramid and olive. Some fibres are said to be derived through the raphe from the nucleus of the other side.

In addition to the hypoglossal nucleus proper, a portion of grey matter, known as the nucleus ambiguus (fig. 268, *n.' am*), projecting into the formatio reticularis of the lateral area of the medulla and co-extensive, according to Laura, with the nucleus of the hypoglossal, is stated by that observer to send fibres through the raphe to the hypoglossal of the opposite side. On the other hand the hypoglossal roots are said by Meynert to be reinforced by the axis-cylinder processes of a group of nerve-cells (anterior or accessory nucleus of the hypoglossal) which lies a little removed from the main nucleus on the ventral aspect, and is traversed by the fibres of the roots. Lastly, in common with all the other nerves, the hypoglossals are supposed to have a crossed communication with the brain through the pyramidal tracts.

Meynert's views of the relations of the parts of the nervous system.—To Professor Meynert of Vienna is due the credit of an attempt to systematize the results of modern investigations into the structure and relations of the various parts of the central nervous system, the attempt being embodied in an idea or scheme of the relations of the parts, which may indeed in many of its details have to undergo modification with the discovery of new facts, but which nevertheless has served and will no doubt continue to serve a useful purpose as a starting-point for renewed attempts to arrange in due order the numerous and complicated details which are constantly accumulating.

Meynert groups the grey substance of the central nervous system into four categories.

1. The superficial grey substance of the cerebral hemispheres.
2. The grey substance of the cerebral ganglia (caudate nucleus, lenticular nucleus, optic thalamus, corpora quadrigemina, locus niger, &c.).
3. The grey substance which surrounds the central cavities of the brain and spinal cord. Commencing above at the infundibulum, it lines the third ventricle and the aqueduct of Sylvius, extends through the fourth ventricle, and surrounds the canal of the spinal cord.
4. The cerebellum and its appendages, including the grey substance in the inferior medullary velum and the pons traversed by its commissural fibres.

If the whole tract of nervous conduction, from the grey matter of the cerebral convolutions, on the one hand, to the peripheral terminations of the nerves of sense and motion on the other, be regarded as a whole, it is seen to traverse the second and third groups of grey substance, viz.: that of the cerebral ganglia, and that of the central grey substance. These divide it into three segments,—an upper, middle, and lower. These three segments are termed *projection-systems*, since the function of the whole nervous tract may be considered as being to project the external world on the cerebral convolutions, and conversely the changes in the cerebral convolutions upon the motor organs.

The *first projection system* between the convolutions and the cerebral ganglia (corpus striatum, &c.), corresponds for the most part to the corona radiata.

The *second projection system* connects the cerebral ganglia to the central grey matter. As the latter extends from the third ventricle to the lower end of the spinal cord, the fibres of this system are of very various lengths.

The *third projection system*, from the grey matter of the central cavities to the muscles and terminations of the sensory nerves, corresponds nearly to the peripheral nerves.

The other systems of fibres are (as commonly enumerated) the *commissural*, such as the corpus callosum and anterior commissure, which unite identical

regions of different hemispheres, and the *association-system* of fibres which unite non-identical regions of the same hemisphere.

In regard to the passage from the first to the second projection-system, which is supposed to be effected in the cerebral ganglia, it should be remarked that, since it has been shown that the fibres of the pyramidal tract pass directly to the cerebral cortex without traversing the cerebral ganglia, it is clear that an exception must be made for these fibres at least, if not for others. The fibres undergo considerable reduction in number in passing from the first to the second system, the fibres of the crus being much fewer than those of the corona radiata. On the other hand, in the transition from the second to the third projection-systems, in the grey substance of the central cavities, the fibres undergo a great increase in number: the peripheral nerve-fibres being much more numerous than those of the crus or of the cord.

The division of the fibres of the crus into two portions, an anterior or lower (*crustal*), and an upper or posterior (*tegmental*), may be extended to the cerebral ganglia, in which the fibres of each portion respectively terminate above. The ganglia connected with the crusta are the lenticular nucleus, the caudate nucleus and substantia nigra; or this latter may be connected with an intermediate set of fibres belonging neither to the crustal nor to the tegmental set. They are connected (by part of the first projection-system) chiefly with the anterior part of the brain, and subserve for the most part voluntary motion. The ganglia of the tegmentum are the optic thalami, corpora quadrigemina, corpora geniculata interna, and corpora albicantia, and subserve chiefly reflex movements.

Certain fibres, which are thought to be sensory, pass up from the posterior columns of the cord, and form the posterior and outer fasciculi of the crusta. They pass through no ganglion, but ascend behind the optic thalamus to the cortex of the temporal lobe.

The cerebellar grey substance is regarded by Meynert as forming a special central organ shunted in between the cerebrum and the spinal cord and connected with the cord by the inferior peduncle, with the cerebrum by two groups of fibres, viz.:—(1). Those of the connecting arm, processus a cerebello ad cerebrum, or superior peduncle, which pass from the corona radiata, under the thalamus and corpora quadrigemina, to mix with the fibres of the tegmentum, and reach the cerebellum after a total decussation. (2). Some of the fibres of the crusta, which, as they are prolonged downwards through the pons, turn aside in the latter and reach the cerebellum through the middle peduncle. To this circumstance is due the fact that the size of the crusta above the pons, is much greater than that of the motor tract into which it is continued below.

THE MEMBRANES OF THE BRAIN AND SPINAL CORD.

The cerebro-spinal axis is covered by three *membranes*, named also *meninges*. They are:—1. An external fibrous membrane, named the *dura mater*, which lines the interior of the skull, and forms a loose sheath in the spinal canal; 2. An internal areolar vascular tunic, the *pia mater*, which closely covers the brain and spinal cord; and 3. An intermediate non-vascular membrane, the *arachnoid*, which lies over the pia mater, the two being in some places in close connection, in others separated by a considerable space.

THE DURA MATER.

The dura mater is a very strong dense inelastic fibrous tunic of considerable thickness. Its inner surface, turned towards the brain and spinal cord, is smooth and lined with epithelium, which was formerly regarded as a parietal reflection of the arachnoid membrane, this having been generally looked upon as a serous membrane. The space between the dura mater and arachnoid was formerly in like manner regarded as the sac of the arachnoid, but is now conveniently termed the *subdural*

space. The outer surface of the dura mater is connected with the surrounding parts, in a somewhat different manner in the cranium and in the spinal canal.

In the cranium it adheres to the inner surface of the bones, and forms their internal periosteum. The connection between the two depends, in a great measure, on blood-vessels and small fibrous processes, which pass from one to the other; and the dura mater, when detached and allowed to float in water, presents a flocculent appearance on its outer surface, in consequence of the torn parts projecting from it. The adhesion between the membrane and the bone is more intimate opposite the sutures, and also at the base of the skull, which is uneven, and perforated by numerous foramina, through which the dura mater

Fig. 317.

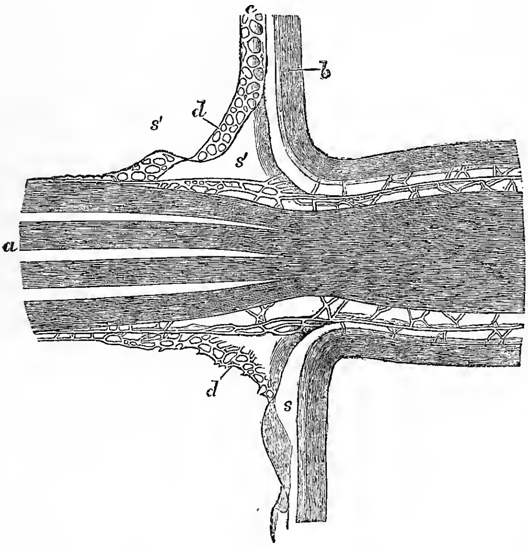


Fig. 317.—SECTION THROUGH THE PLACE OF EXIT OF A SPINAL NERVE-ROOT THROUGH THE DURA MATER. (Key and Retzius.)

a, bundles of the nerve-root becoming collected into a single bundle as they emerge; *b*, dura mater; *c*, arachnoid; *d*, a reticular lamella of the arachnoid reflected along the nerve-root; *s*, subdural space; *s′*, *s′*, subarachnoid space.

is prolonged to the outer surface, being there continuous with the pericranium. The fibrous tissue of the dura mater becomes blended with the areolar sheath of the nerves at the foramina which give exit to them.

In leaving the skull, the dura mater is intimately attached to the margin of the foramen magnum; but within the vertebral canal it forms a loose sheath around the cord (*theca*), and is not adherent to the bones, which have an independent periosteum. Towards the lower end of the canal, a few fibrous slips proceed from the outer surface of the dura mater to be fixed to the vertebræ. The space intervening between the wall of the canal and the dura mater is occupied by loose fat, by areolar tissue, and by a plexus of spinal veins.

Opposite each intervertebral foramen the dura-matral theca presents two openings, placed side by side, which give passage to the two roots of the corresponding spinal nerve. It is continued as a tubular prolongation on the nerve (fig. 317), and is lost in its sheath. Besides this, it is connected with the circumference of the foramen by areolar tissue.

The fibrous tissue of the dura mater, especially within the skull, is divisible into two distinct layers, and at various places the layers

separate from each other and leave intervening channels, called *sinuses.* These sinuses, which have been elsewhere described, are channels for venous blood, and are lined with a continuation of the internal coat of the veins. The division into two layers is most complete at the base of the skull, in the middle fossa, and in the neighbourhood of the cavernous sinus; on the outer side of this the Gasserian ganglion is included between the two layers. Between the two cavernous sinuses the pituitary body is received into a depression of the membrane, which closely surrounds the organ in question, except where the infundibulum enters it. There is further a fissure immediately over the orifice of the acquæductus vestibuli, and here the prolongation of the membranous labyrinth of the ear, known as the saccus endolymphaticus, is received between the two layers.

The dura mater also sends inwards into the cavity of the skull three strong membranous *processes* or *partitions* formed by duplication of its inner layer. Of these, one descends vertically in the median plane, and is received into the longitudinal fissure between the two hemispheres of the cerebrum. This is the *falx cerebri.* The second is a sloping vaulted partition, stretched across the back part of the skull, between the cerebrum and the cerebellum, named the *tentorium cerebelli.* Below this, another vertical partition, named *falx cerebelli,* of small extent, passes down between the hemispheres of the cerebellum.

The **falx cerebri** (fig. 318, 1) is narrow in front, where it is fixed to the crista galli, and broader behind, where it is attached to the middle of the upper surface of the tentorium, along which line of attachment the straight sinus is situated. Along its upper convex border, which is attached to the middle line of the inner surface of the cranium, runs the superior longitudinal sinus. Its under edge is free, and reaches to within a short distance of the corpus callosum, approaching nearer to it behind. This border contains the inferior longitudinal sinus.

The **tentorium**, or **tent** (fig. 318, 8), is elevated in the middle, and declines downwards in all directions towards its circumference, thus following the form of the upper surface of the cerebellum. Its inner border is free and concave, and leaves in front of it an oval opening, through which the isthmus encephali extends. It is attached behind and at the sides by its convex border to the horizontal part of the crucial ridges of the occipital bone, and there encloses the lateral sinuses. Farther forward it is connected with the upper edge of the petrous portion of the temporal bone—the superior petrosal sinus running along this line of attachment. At the point of the pars petrosa, the external and internal borders meet, and may be said to intersect each other—the former being then continued inwards to the posterior, and the latter forwards to the anterior clinoid process.

The **falx cerebelli** (falx minor, fig. 318, 13) descends from the middle of the posterior border of the tentorium, with which it is connected, along the vertical ridge named the internal occipital crest towards the foramen magnum, bifurcating there into two smaller folds. Its attachment to the bony ridge marks the course of the posterior occipital sinus or sinuses.

Structure.—The dura mater consists of white fibrous and elastic tissue, arranged in bands and laminæ, those of the two layers crossing each other obliquely for the most part in the cranial dura mater. In the spinal dura mater the bundles have a more nearly parallel arrangement. A layer of flattened epitheloid cells covers its inner surface, and also its

outer surface between the places of adherence to the bones and sutures. A similar layer of cells also covers both sides of the spinal dura mater. The cranial membrane is traversed by numerous blood-vessels which are chiefly destined for the bones, but there is a wide meshed capillary network with peculiar ampullary enlargements, distributed near the inner surface of the cranial dura mater. The spaces between the fibrous trabeculæ contain flattened connective tissue corpuscles which frequently

Fig. 318.

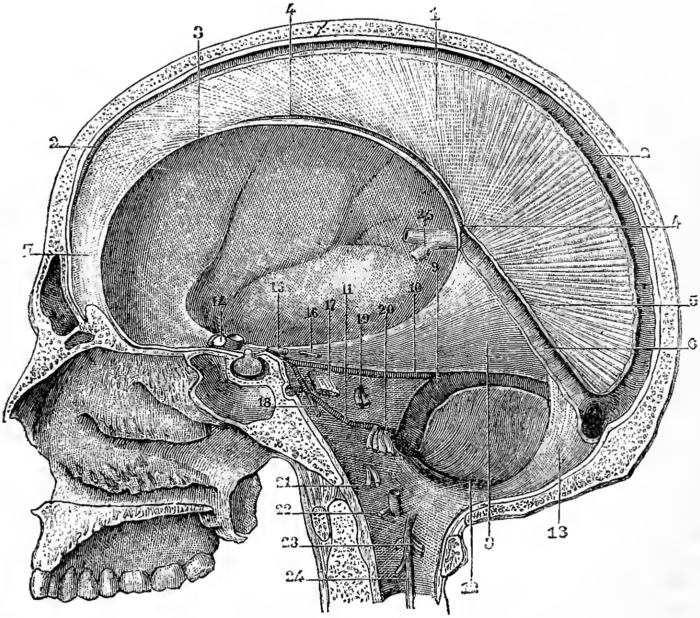


Fig. 318.—The cranium opened to show the falx of the cerebrum and tentorium of the cerebellum, and the places of exit of the cranial nerves. (Sappey). ½

1, falx; 2, superior longitudinal sinus; 3, concave border of the falx; 4, inferior longitudinal sinus; 5, base of the falx; 6, straight sinus; 7, anterior part of the falx; 8, right side of the tentorium cerebelli, seen from below; 9, lateral sinus; 10, superior petrosal sinus; 11, inferior petrosal sinus; 12, posterior occipital sinus; 13, falx cerebelli; 14, 15, 16, 17, 18, second, third, fourth, fifth, and sixth cranial nerves; 19, seventh and eighth nerves; 20, ninth, tenth, and eleventh nerves; 21, twelfth nerve; 22, 23, first and second cervical nerves; 24, upper end of the ligamentum denticulatum.

have an epithelioid arrangement: these spaces, like those of connective tissue generally, doubtless serve for the passage of lymph. They can be injected from the epidural space where this exists, and the injecting fluid can be forced along them through the thickness of the dura mater into the subdural space. They can also be filled by inserting the injecting cannula into the substance of the membrane. Minute nervous filaments, derived from the fifth and twelfth cranial nerves, and from the sympathetic, enter the dura mater of the brain to be distributed chiefly to the blood-vessels and to the bone, but partly perhaps to the membrane itself. Nervous filaments have likewise been traced into the dura mater of the spinal column.

THE PIA MATER.

The pia mater is a delicate, fibrous, and highly vascular membrane, which immediately invests the brain and spinal cord.

Upon the hemispheres of the brain it is applied to the entire cortical surface of the convolutions, and dips into all the sulci, which thus contain a double layer. From its internal surface numerous small vessels pass into the substance of the brain, and hence this inner surface is very flocculent, and is named *tomentum cerebri.* On the cerebellum a similar arrangement exists, but the membrane is finer, and the double fold only distinct in the larger sulci. The pia mater also at the transverse fissure is invaginated into the lateral ventricles and over the third ventricle (covered however by the epithelium of those cavities), and there forms the velum interpositum or tela choroidea superior and choroid plexuses. It is also prolonged over the posterior wall or roof of the fourth ventricle, where it forms the so-called tela choroidea inferior and choroid plexuses of that ventricle.

On the spinal cord the pia mater has a very different character from that which it presents on the encephalon, so that it has even been described by some as a different membrane under the name *neurilemma of the cord.* It is thicker, firmer, less vascular, and more adherent to the subjacent nervous matter: its greater strength is owing to an external fibrous layer, which is arranged in longitudinal glistening bundles. A fold of this membrane dips down into the anterior fissure of the cord, and serves to conduct blood-vessels into that part. A thinner process passes into the greater part of the posterior fissure. At the roots of the nerves, both in the spine and in the cranium, the pia mater becomes continuous with their connective tissue sheaths.

The pia mater of the cord is thickened by a conspicuous fibrous band, running down in front over the anterior median fissure. This was named by Haller *linea splendens.*

Structure.—The pia mater of the cord consists of two layers, the outer one being composed of interlaced bundles of connective tissue, which are for the most part parallel and longitudinal, and the inner or intima of peculiar stiff bundles bending suddenly and enclosing somewhat angular interspaces. Both surfaces of this inner layer are covered with epithelioid cells, and there is a network of fine elastic fibres near the surfaces. On the cord pigmented cells are sometimes scattered among the elastic fibres. The outer and inner layers are separated here and there by cleft-like lymphatic spaces communicating on the one hand with the subarachnoid space and on the other with the perivascular canals immediately to be mentioned. In the pia mater of the brain only the inner of the two layers of the pia mater of the cord is represented.

The pia mater contains great numbers of blood-vessels, which subdivide in it before they enter the nervous substance. In the pia mater of the cord they lie between its two layers, but in that of the brain on the surface of the membrane, either projecting freely or covered by subarachnoid trabeculæ. Further each vessel is enclosed by a sheath composed of a more dense arrangement of the fibres of the membrane (perivascular sheath). The diameter of the (lymphatic) canal thus formed may be considerably larger than that of the contained vessel. A similar sheath, derived from the pia mater, accompanies the vessel into the substance of the brain. At its commencement it is loose and funnel-shaped and

can be injected from the subarachnoid cavity. On the cerebrum the inner layer of the pia mater is more closely adherent to the cortical substance of the convolutions, than on the cerebellum ; where a distinct space traversed by fibres exists between the two.

Nerves.—Purkinje described a retiform arrangement of fine nerve-fibres in the pia mater ; these are derived, according to Kölliker and others, from the sympathetic, and from the third, fifth, sixth, facial, pneumogastric, glossopharyngeal, and accessory nerves. Most of the fibres are destined in all probability for the blood-vessels.

The spinal pia mater is supplied by nerves from the sympathetic.

The arrangement and structure of the choroid plexuses have already been described.

THE ARACHNOID MEMBRANE.

The arachnoid is a delicate membrane which is situated outside the pia mater, and invests the brain and spinal cord much less closely than that membrane. It passes over the various eminences and depressions on the cerebrum and cerebellum, without dipping down into the sulci and smaller grooves. Beneath it, between it and the pia mater, is a space (subarachnoid space) in which is a considerable quantity of fluid (subarachnoid fluid), and in which are seen the larger blood-vessels passing obliquely towards the brain.

The **subarachnoid space** is larger and more evident in some places than in others. Thus, in the longitudinal fissure, the arachnoid does not descend to the bottom, but passes across, immediately below the edge of the falx, at some distance above the corpus callosum. In the interval thus left, the arteries of the corpus callosum run backwards along that body. At the base of the brain and in the spinal canal there is a wide interval between the arachnoid and the pia mater. In the base of the brain, this subarachnoid space extends in front over the pons and the interpeduncular recess as far forwards as the optic nerves, and behind it forms a considerable interval between the cerebellum and the back of the medulla oblongata (fig. 319). In the spinal canal, where it surrounds the cord, it is of considerable extent. It is occupied, in both brain and cord, by trabeculæ and thin membranous extensions of delicate connective tissue, connected on the one hand with the arachnoid, and on the other with the pia mater. This tissue is most abundant where the space between the two membranes is least. It is dense in the neighbourhood of the vessels, and is continuous with the tissue of their walls. In the subarachnoid space at the base of the brain in several places the arachnoid is separated by larger intervals than at other parts from the pia mater.

The subarachnoid space communicates with the ventricles of the brain by means of the foramen of Magendie (fig. 319, *f M*), the opening into the lower part of the fourth ventricle, through the pia-matral expansion (tela choroidea inferior) which closes it. Two other openings through this membrane exist, one on each side, behind the upper roots of the glossopharyngeal nerve, in the pouch-like extension of the membrane beneath the flocculus.

A certain quantity of fluid is contained between the arachnoid membrane and the dura mater ; but the chief part of the cerebro-spinal fluid is lodged in the subarachnoid space in the meshes of the trabecular tissue.

The spinal subarachnoid space (fig. 320, *k, l*) is divided by an imperfect fibrous septum on either side termed the ligamentum denticulatum (*g*) into anterior and posterior portions. As was pointed out by Magendie there also exist a sort of septum dividing the subarachnoid space at the back of the cord (*septum posticum* (*c*)), the relations of which have been carefully studied by Axel Key and Retzius. It is a thin membranous partition, which passes in the median plane from the pia mater covering the posterior median fissure of the cord to the opposite part of

Fig. 319.

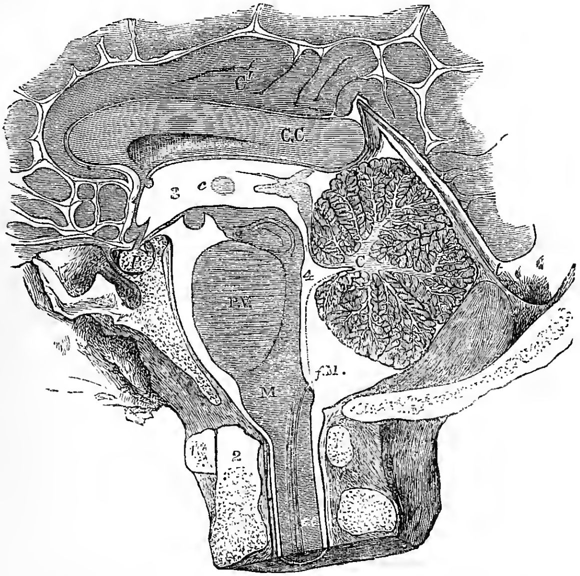


Fig. 319.—Section of the posterior and lower parts of the brain within the skull, to exhibit the subarachnoid space, and its relation to the ventricles. (After Key and Retzius.)

The section was made in the frozen state, the cavities having been previously filled with injection.

1, 1', atlas vertebra; 2, odontoid process of the axis, 2'; 3, third ventricle; 4, fourth ventricle; *C, C*, corpus callosum? *C'*, gyrus fornicatus; *C*, cerebellum; *t*, tentorum; *p*, pituitary body; *c, c*, central canal of the cord; *fM*, in the cerebello-medullary part of the subarachnoid space, is close to the foramen of Magendie by which that space communicates with the fourth ventricle.

the loose portion of the arachnoid membrane. It is most perfect in the cervical region, being incomplete below. It consists of numerous fine lamellæ, enclosing between them small spaces, within which run the larger blood-vessels. Subarachnoid trabeculæ also connect the nerve-roots with the inner surface of the arachnoid, and in the dorsal region fine membranous trabeculæ extend between the posterior nerve-roots and the posterior septum. In most parts however the subarachnoid trabeculæ are far less developed in the spinal canal than in the cranium.

The nerves as they pass from the brain and spinal cord receive their

perineural covering from the pia mater, and, in addition, two looser sheaths, an outer from the dura mater, and an inner from the arachnoid (fig. 317). Upon the optic nerve these sheaths remain distinct and separate, so that the space which each encloses may be injected, the outer

Fig. 320.

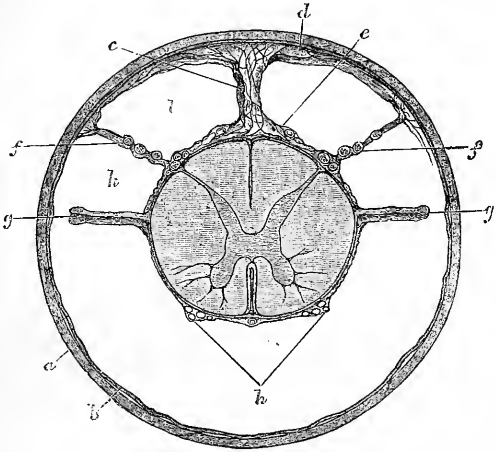


Fig. 320.—SECTION OF THE SPINAL CORD WITHIN ITS MEMBRANES (UPPER DORSAL REGION). (Key and Retzius). Magnified.

a, dura mater ; *b*, arachnoid ; *c*, septum posticum ; *d*, *e*, *f*, subarachnoid trabeculæ, those at *f*, *f*, supporting bundles of a posterior nerve-root ; *g*, ligamentum denticulatum ; *h*, sections of bundles of an anterior nerve-root ; *k*, *l*, subarachnoid space.

from the subdural, the inner from the subarachnoid space. On the other nerves the arachnoidal sheath soon ceases, and the single sheath eventually blends with both the epineurium and perineurium of the nerves. Accordingly it is found that injection driven into either the subdural or the subarachnoid space passes readily along the nerves even as far as the limbs. There thus exists a continuity between the ventricles of the brain, the subarachnoid space, the perivascular canals of the cerebral substance, and the lymphatic spaces within the nerve-sheaths.

Structure.—When examined under the microscope, the arachnoid membrane is found to consist of distinct riband-like bundles of fine fibrous tissue interlaced with one another. The intervals between these bundles are filled up by delicate membranes, composed of expanded cells, the nuclei of which persist and are scattered over the structure. Several layers of this tissue, arranged in a complex way, constitute the arachnoid membrane. The subarachnoid trabeculæ consist of bundles of similar fine fibrillar tissue, each of which is surrounded by a delicate nucleated sheath, also composed of cells, and continuous with the intertrabecular cell-membranes of the arachnoid itself. The finer trabeculæ when swollen by acetic acid very frequently show the well-known ring-like constrictions. The subarachnoid membranous expansions have a similar structure. In the spinal arachnoid the fibril-bundles have for the most part a longitudinal direction.

Volkmann described a rich plexus of nerves in the arachnoid membrane of certain ruminants. Kölliker failed to detect their presence ; but they have been again described by Bochdalek, who traces them to the portio minor of the fifth, the facial, and accessory nerves ; and they have likewise been followed by Luschka.

Ligamentum Denticulatum.—This is a narrow fibrous band which runs along each side of the spinal cord in the subarachnoid space, between the anterior and posterior roots of the nerves, commencing above at the foramen magnum,

and reaching down to the lower pointed end of the cord (fig. 244, 9, and fig. 320, *g*). By its inner edge this band is connected with the pia mater of the cord, while its outer margin is widely denticulated ; its denticulations are attached by their points to the inner surface of the dura mater, and thus serve to support the cord along the sides, and to maintain it in the middle of the cavity. The first or highest denticulation is fixed opposite the margin of the foramen magnum, between the vertebral artery and the hypoglossal nerve; the others follow in order, alternating with the successive pairs of spinal nerves. In all, there are about twenty-one of these points of insertion, but the lower six or seven are less regular. The points of the lower denticulations are prolonged into threads, and ascend slightly to their attachments. At the lower end, the ligamentum denticulatum may be regarded as continued into the terminal filament of the spinal cord, which thus connects it to the dura mater at the extremity of the sheath. The free edge, in the intervals between the denticulations, is slightly thickened, and in many parts is closely applied to the inner surface of the arachnoid, with which it is often directly connected by fine trabeculæ. The denticulations do not

Fig. 321.

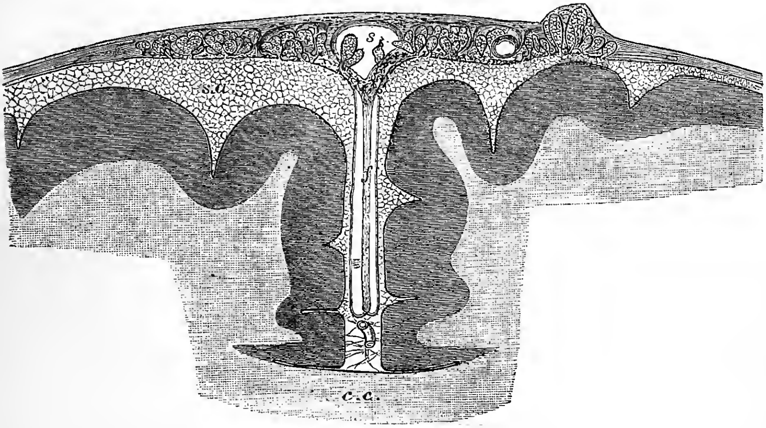


Fig. 321.—Section of the upper part of the brain and meninges to show the relations of the arachnoidal villi. (Key and Retzius). Magnified.

c. c, corpus callosum ; *f*, falx cerebri ; *s. a*, subarachnoid space, pervaded by a network of fine trabeculæ ; from it the fungiform villi are seen projecting into the dura mater. Some are projecting into the superior longitudinal sinus, *s*.

perforate the arachnoid but receive from it funnel-shaped sheaths, which accompany them to the inner surface of the dura mater (Axel Key and Retzius).

In structure the ligament consists of white fibrous tissue, mixed with many exceedingly fine elastic fibres. Several layers of fine connective tissue trabeculæ may be traced : they are surrounded by sheaths, which are composed of delicate nucleated cells, and here and there expand into membranes. Its tissue is continuous on the one hand with that of the pia mater, and at the apices of the denticulations with that of the dura mater.

Glandulæ Pacchionii or arachnoidal villi.—Upon the external surface of the dura mater, in the vicinity of the longitudinal sinus, are seen numerous small pulpy looking elevations, generally collected into clusters, named glands of Pacchioni (fig. 321). The inner surface of the calvarium is marked by little pits, which receive these prominences. Similar excrescences are seen on the internal surface of the dura mater, and upon the pia mater on each side of the longitudinal sinus, and also projecting into the interior of that sinus (*s*). Occasionally they are found also in other situations.

On a careful examination of the connections of these bodies it will be found that the elevations found on the outer surface of the dura mater and within the longitudinal sinus, in no instance take origin in those positions, but that they are grape-like bodies which are attached more deeply, and in their growth have perforated the dura mater. Their precise origin and nature were long the subject of conflicting opinions, but it has been satisfactorily shown by Luschka that they are only an enlarged condition of normal villi of the arachnoid. On each side of the sinus, and communicating with it, are large venous spaces in the dura mater; into these the villi project even in new-born animals, and those which perforate the dura mater and appear on the surface have their inner parts in these spaces. Each villus is covered by a membrane, continuous with the arachnoid. Outside this is another fine membranous sheath, derived from the dura mater, and the interval between the two is continuous with the subdural space. Within the villus is a spongy trabecular tissue, continuous with the subarachnoid tissue, and of similar structure (Key and Retzius).

Fluid injected into the subarachnoid space passes freely into the Pacchionian bodies, and is found after a time to filter through their walls and thus to get into the subdural space, although there does not appear to be any open communication between the interior of these bodies and the prolongation of the subdural space which surrounds them. Moreover, if the injection is continued it can be driven even into the interior of the venous sinuses and lacunæ which are found in connection with them, especially into the superior longitudinal sinus, into which the arachnoidal villi project. So that these villi seem to afford a means of passage of the cerebro-spinal fluid from the subarachnoid space into the venous sinuses, when the fluid pressure in the subarachnoid space becomes from any cause increased above the normal.

BLOOD-VESSELS OF THE BRAIN AND SPINAL CORD.

Blood supply of the spinal cord.—The arteries of the spinal cord are (1) the anterior spinal, double above where it is derived from the vertebrals, but single and median below where it is reinforced by a series of small vessels derived from the vertebral, intercostal, lumbar, and other arteries; and (2) the paired posterior spinal arteries, similarly derived, and running just behind the line of attachment of the posterior roots. The branches of these vessels ramify in the pia mater investing the cord, and from the main vessels and their ramifications vessels pass in to supply both the grey and white substance.

The small entering branches may be described as forming two systems, a centrifugal and a centripetal. The first is composed of a series of arterioles, 250 to 300 in number, which pass from the anterior spinal artery into the anterior median fissure, penetrating to the anterior commissure. Here each one divides into a right and left branch, which again divide into smaller arteries and capillaries for the central parts of the corresponding crescent of grey matter; but an ascending and a descending ramuscle is also given off on either side for anastomosis with the corresponding vessels above and below.

The second or centripetal set have a converging or radial arrangement, passing in from the periphery. Some of these simply form capillary loops, which supply the superficial layers of the cord. Others are distributed to the white matter, where they form comparatively large-meshed longitudinal plexuses. But the most considerable of the centripetal arteries penetrate to the grey matter, and pour their blood into the close capillary network which pervades it, supplying the parts not served by the centrifugal vessels. Special mention may be made of a series of small median arterial branches which enter the posterior fissure, penetrating in it to the posterior commissure, and giving off branches which supply the adjacent parts of the posterior white columns and Clarke's column, where this is found; and of the vessels which enter the grey matter with the bundles of the anterior and posterior nerve-roots, and are distributed to the corresponding cornua.

The veins run alongside the arteries. Two longitudinal venous vessels, one on either side of the central canal, accompanying the corresponding anastomotic

arteries, are conspicuous in most transverse sections of the cord. (For further details see Adamkiewicz in Trans. Internat. Med. Congress, London, 1881, and in Wiener Sitzungsberichte, 1881 and 1882.)

Blood supply of the brain.—The origin and course of the vessels which supply the brain have already been described in the Section Angeiology, Vol. I. In passing to their distribution the several arteries, having passed across the arachnoid cavity, enter the subarachnoid space and then divide and subdivide into branches, which, in their further ramification in the nervous centres, are supported by the pia mater, and, it may be remarked, are more deeply placed in the various fissures and sulci than the small veins, which do not accompany the arteries, but pursue a different course and are chiefly seen upon the surface of the pia mater. From the arteries in the pia mater of the hemispheres very numerous small branches pass vertically into the grey matter of the convolutions. Most of these (*cortical arteries*) at once break up into a close plexus of capillaries for the grey matter; but others (*medullary arteries*), larger but less numerous, pass through the grey matter, giving off only a few small branches to it, and penetrate for some distance into the medullary centre, where they divide into a long meshed capillary network. The smaller branches of arteries anastomose together to a certain extent in the pia mater before penetrating into the superficial grey matter, but the branches which pass to the chief ganglia, such as the optic thalamus or corpus striatum, do not anastomose with one another except by their capillary branches (End-arterien of Cohnheim).

Moreover, it is to be observed that, whilst the main branches of the arteries are situated at the base of the brain, the principal veins tend towards the upper surface of the hemispheres, where they enter the superior longitudinal sinus: the veins of Galen, however, coming from the lateral ventricles and choroid plexuses, run backwards to the straight sinus, in the subarachnoid tissue which lies between the two layers of the velum interpositum.

It may be convenient here to recapitulate the sources of the blood supply to the several parts of the encephalon.

The **medulla oblongata and pons Varolii** are supplied by branches from the anterior spinal, the vertebral, the basilar, and the posterior cerebral arteries. The branches enter the pons and medulla in two sets, lateral or radicular (following the roots of the nerves), and median,—the latter passing in the septum to the grey matter on the posterior surface. The valve of Vieussens and the superior peduncle of the cerebellum receive twigs from the superior cerebellar arteries. The choroid plexuses of the fourth ventricle are supplied by the posterior inferior cerebellar arteries.

Cerebellum.—The *under surface* is supplied by the posterior inferior cerebellar arteries from the vertebral, and the anterior inferior from the basilar. The *upper surface* is supplied chiefly by the superior cerebellar arteries from the basilar: its posterior portion from the posterior inferior cerebellar.

The **crura cerebri** derive their blood supply from the posterior communicating and the posterior cerebral arteries. Branches of the latter, and also others from the end of the basilar, enter the posterior perforated space.

The **corpora quadrigemina** and **corpora geniculata** are both supplied by the posterior cerebral artery, but branches of the superior cerebellar arteries pass to the inferior corpora quadrigemina.

The **optic thalamus** is supplied above and on the outer and posterior side by branches of the posterior cerebral artery, but its anterior and inner portions receive twigs from the anterior and posterior communicating arteries of the circle of Willis.

Cerebral hemispheres.—*Frontal lobe.*—The superior frontal and anterior two-thirds of the middle frontal convolution, with the upper extremity of the ascending frontal, are supplied by the anterior cerebral. The inferior frontal convolution, the posterior extremity of the middle frontal, and the greater part of the ascending frontal convolutions are supplied by the middle cerebral. The orbital surface is supplied, outside the orbital sulcus, by the middle cerebral: within that sulcus (including the olfactory bulb) by the anterior cerebral.

Parietal lobe.—All the convolutions of the parietal lobe are supplied by the middle cerebral artery.

Occipital lobe.—This lobe is supplied by the posterior cerebral artery.

Temporo-sphenoidal lobe.—The superior, and upper part of the middle temporo-sphenoidal convolutions are supplied by the middle cerebral artery. The lower portion of the lobe by the posterior cerebral.

Inner surface of the hemispheres.—The whole anterior and upper portion, as far back as the parieto-occipital fissure, is supplied by the anterior cerebral artery; the cuneate lobule and the occipito-temporal region by the posterior cerebral.

The *corpus callosum* is chiefly supplied by the anterior cerebral.

The *grey substance at the base* of the cerebrum is supplied by small twigs from the adjacent vessels of the circle of Willis, or from the roots of the cerebral vessels which pass off from that anastomosis.

Central parts—corpus striatum.—Both nucleus caudatus and nucleus lenticularis are supplied almost exclusively by the middle cerebral artery, the numerous branches to these parts entering through the foramina in the anterior perforated space. The anterior part of the caudate nucleus is also supplied by the anterior cerebral, and its upper surface receives fine twigs from the lateral choroidal branch of the posterior cerebral.

For further details on the subject, which derives importance from the relation of different local pathological conditions to the vascular distribution, the reader is referred to a series of articles by Duret in the Archives de Physiologie for 1873 and 1874, to a paper by Heubner in the Med. Centralblatt, 1872; and to a work entitled "Die luetische Erkrankung der Hirnarterien," Leipzig, 1874, by the same author.

Lymphatics.—The lymphatics of the brain and spinal cord appear to originate in the form of perivascular clefts in the adventitia, or outer coat of the blood-vessels. The clefts in question communicate both with lymphatic spaces in the pia mater, and with the subarachnoid space. The fine meshes of the neuroglial reticulum which are much more distinct in some parts than in others, the pericellular spaces which are thought to be in communication with those meshes, and a cleft-like space, which can be injected, between the pia mater and the surface of the spinal cord and brain (*subpial space*, *epicerebral space*), have also been regarded as forming part of the lymphatic system of the central nervous organs.

SIZE AND WEIGHT OF THE ENCEPHALON.

The average weight of the brain is about 49½ oz. (1400 grammes) in the male, and 5 to 5½ oz. less in the female.

The results obtained by Sims, Clendinning, Tiedemann, and J. Reid show the maximum weight of the adult male brain, in a series of 278 cases, to be 65 oz., and the minimum weight 34 oz. In a series of 191 cases, the maximum weight of the adult female brain was 56 oz., and the minimum 31 oz.; the difference between the extreme weights in the male subject being no less than 31 oz., and in the female 25 oz. In a very large proportion the weight of the male brain ranges between 46 oz. and 53 oz., and that of the female brain between 41 oz. and 47 oz. The *prevailing* weights of the adult male and female brain may therefore be said to range between those terms; and, by taking the mean, an *average* weight is deduced of 49½ oz. for the male, and of 44 oz. for the female brain,—results which correspond closely with the statements generally received.*

Although many female brains exceed in weight particular male brains, as a general fact it may be affirmed that the adult male encephalon is heavier than

* Tables exhibiting at greater length the results obtained by the observers above mentioned, and also those obtained by R. Boyd of the weight of the brain at different ages, will be found in previous editions of this work. The reader is also referred to the papers by Peacock in the Edin. Med. Journal for 1847, and Journ. of the Pathol. Society, 1860, to the elaborate table of Rud. Wagner in his "Vorstudien, &c.," 1860, and to a recent work by Bischoff (Hirngewicht des Menschen, Bonn, 1880).

that of the female. In new-born infants the brain was found by Boyd to weigh on an average 11.65 oz. in the male, and 10 oz. in the female.

The observations of Sims, Tiedemann, and Reid, appear to show that in both sexes the weight of the brain in general increases rapidly up to the seventh year, then more slowly to between sixteen and twenty, and again more slowly to between thirty-one and forty, at which time it reaches its maximum point. Beyond that period there appears a slow but progressive diminution in weight, amounting to about 1 oz., during each subsequent decennial period; thus confirming the opinion that the brain diminishes in advanced life. According to Peacock and Bischoff, the maximum weight of the brain is attained between the ages of twenty and thirty years.

Race exercises a considerable influence upon the size of the brain; thus it is largest in Europeans and Chinese; smaller in Hindoos, Bushmen and Negritoes (partly in relation to the small prevailing stature) and natives of Australia; intermediate in size between these in North American Indians and Negroes.

The *relative weight of the encephalon to the body* is liable to great variation; nevertheless, the facts to be gathered from the observations of Clendinning, Tiedemann, and Reid, furnish the following general result. In a series of 81 males, the average proportion between the weight of brain and that of the body at the ages of twenty years and upwards, was found to be as 1 to 36·5; and in a series of 82 females, to be as 1 to 36·46. The results of Bischoff's observations give 1 to 35.2 in the female. In these cases the deaths were the result of more or less prolonged disease; but in healthy individuals dying suddenly from disease or accident, the average proportion is probably 1 to 45.

The proportionate weight of the brain to that of the body is much greater at birth than at any other period of life, being, according to Tiedemann, about 1 to 5·85 in the male, and about 1 to 6·5 in the female. From the observations already referred to, it further appears that the proportion diminishes gradually up to the tenth year, being then about 1 to 14. From the tenth to the twentieth year, the relative increase of the body is most striking, the ratio of the two being at the end of that period about 1 to 30. After the twentieth year, the general average of 1 to 36·5 prevails, with a further trifling decrease in advanced life.*

The attempts hitherto made to measure or estimate the relative proportions of the different convoluted parts of the cerebrum to each other and to the degree of intelligence, either more directly or by the craniospic methods, have been attended with little success. Such researches as those of Rudolph Wagner give, however, some promise, when fully carried out, of affording more definite results. These researches had for their object to institute an accurate comparison between the brains of certain persons of known intelligence, cultivation, and mental power, and those of persons of an ordinary or lower grade. As examples of brains of men of superior intellect he selected those of Professor Gauss, a well-known mathematician of eminence, and Professor Fuchs, a clinical teacher; and as examples of brains of ordinary persons, those of a woman of 29 and a workman.

The careful measurement of all the convolutions and the intervening grooves in the four brains above mentioned has been carried out by H. Wagner, and the result of these measurements is partly given in the accompanying table (see next page), the numbers indicating square inches of surface.

It will be seen that although there are undoubtedly differences in the brains examined, these are by no means so striking as might have been expected. Indeed it may be stated that the general result of these and similar observations has been hitherto inconclusive, for although there have been observed several notable instances in which superiority of intellect has been found to be accompanied by increased size or complexity of the cerebral surface, in many other cases no such relation has been noticed.

* On the relation between the weight of the brain and the individual stature, see J. Marshall, Proc. Roy. Soc. 1875: le Bon, Rev. d'Anthrop., 1879, and Bischoff, in the work above-mentioned.

Comparative measurement of the extent of surface of the Convolutions of the Cerebrum and its lobes.

	Surface of each lobe separately.				Free and deep surfaces of Cerebrum.		Whole surface of Cerebrum.
	Frontal.	Parietal.	Occipital.	Temporal.	Free surface.	Deep or covered surface.	
1. Gauss	130.	70.6	59.4	68.4	112.8	228.2	341.
2. Fuchs	143.4	69.5	59.	67.5	110.7	231.3	342.
3. Woman	130.	65.	51.	66.8	107.5	209.9	317.5
4. Workman ..	113.2	62.3	50.5	62.	97.4	193.6	291.

WEIGHT OF THE SEVERAL PARTS OF THE ENCEPHALON.

As the result of observations made in reference to this subject, on the brains of 53 males and 34 females, between the ages of twenty-five and fifty-five, Dr. J. Reid has given the following tables :—

	Males.		Females.		Difference.	
	oz.	drs.	oz.	drs.	oz.	drs.
Average weight of cerebrum	43	$15\frac{3}{4}$	38	12	5	$3\frac{3}{4}$
,, cerebellum	5	4	4	$12\frac{1}{4}$	0	$7\frac{3}{4}$
,, pons and medulla oblongata .	0	$15\frac{3}{4}$	1	$0\frac{1}{4}$	0	$0\frac{1}{2}$
,, entire encephalon . .	50	$3\frac{1}{2}$	44	$8\frac{1}{2}$	5	11

With these results the observations of Huschke, and of Weisbech, mainly agree.

From this it appears that the proportionate weight of the cerebellum to that of the cerebrum is, in the male, as 1 to $8\frac{4}{7}$, and in the female, as 1 to $8\frac{1}{4}$.

In the new-born infant the ratio of the weight of the cerebellum to that of the whole brain is strikingly different from that observed in the adult. Huschke found the weight of the cerebellum, medulla oblongata, and pons together in the new-born infant, as compared with that of the brain, to be in the proportion of 1 to 15, and 1 to 13. In the adult the proportions were 1 to 7, and 1 to 6.

Meynert found the proportions between the frontal, parietal, and conjoined occipital and temporo-sphenoidal lobes to be 41·5 : 23·4 : and 35·1.

WEIGHT OF THE SPINAL CORD.

Divested of its membranes and nerves, the spinal cord in the human subject weighs from 1 oz. to $1\frac{3}{4}$ oz. Its proportion to the encephalon is about 1 to 33.

SPECIFIC GRAVITY OF THE ENCEPHALON.

The specific gravity of the different parts of encephalon has of late attracted some attention from the fact having been observed that it varies to some extent in different kinds of disease. From the researches of various observers, it appears that the average specific gravity of the whole encephalon is about 1036, that of the grey matter 1034, and that of the white 1040. There are also considerable differences in the specific gravity of some of the internal parts. Comparing the specific gravity of the white and grey substances respectively with that of the whole brain, Danilewsky has calculated that about 33 per cent. of the weight of the hemispheres is due to the grey cortex, or including the basal ganglia about 35·5 per cent.*

* For the recent literature of the brain and spinal cord the reader is referred to the important work by Schwalbe (Lehrbuch der Neurologie, Erlangen, 1881), where it is given with great completeness, and where many more details regarding the structure of the central nervous system may be found than could conveniently be introduced here. The similar work by Henle (Nervenlehre, Brunswick, 1879) may also be consulted with advantage.

ORGANS OF THE SENSES.

In this place will be described the organs of sight, hearing, and smell —the higher organs of special sense. The description of the organ of touch is given with the skin, and that of the organ of taste with the tongue.

THE EYE.

The organ of vision, strictly speaking, consists only of the ball or globe of the eye ; but connected with the eyeball externally are muscles, nerves, and blood-vessels, elsewhere described, as well as other parts specially destined for its protection, and known as the appendages of the eye (tutamina oculi), of which an account will first be given.

THE EYELIDS AND CONJUNCTIVA.

The eyelids (*palpebræ*) are moveable portions of integument, strengthened towards their margins by a thin lamina of dense fibrous tissue (*tarsus*). A mucous membrane (*conjunctiva*) lines their inner surface, and is reflected thence on the front of the eyeball. The line of reflection is termed the *fornix* of the conjunctiva.

Fig. 322.

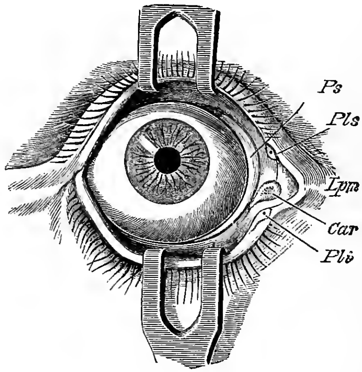


Fig. 322.—Front view of the right eye, with the eyelids drawn apart by blunt hooks (Merkel).

Ps, plica semilunaris ; *Pls*, *Pli*, punctum lachrymale sup. et inf. ; *Car*, caruncula lachrymalis ; *Lpm*, internal tarsal ligament.

The upper lid is larger and more moveable than the lower, all the transparent part of the globe being covered by it when the eye is closed; it is chiefly by the elevation of this lid that the eye is opened, the movement being effected by a muscle (*levator palpebræ*) devoted exclusively to this purpose. At the outer and inner angles (*canthi*) of the eye the eyelids are united. The interval between the angles varies in different individuals, and, according to its extent, gives the appearance of a larger or a smaller eye, the size of the globe being nearly the same in all. The greater part of the edge of each eyelid is flattened and angular, but towards the inner canthus it is rounded off for a short space, at the same time that it changes its direction ; at this point there is seen on each lid a slight elevation (*papilla lachrymalis*,)—the apex of which is pierced by the aperture (*punctum*) of a small canal (*canaliculus lachrymalis*) which serves to convey away the fluid which moistens the conjunctiva (fig. 322, *Pli*).

In the greater part of their extent the lids are applied to the surface of the eyeball ; but at the inner canthus, opposite the apertures, there intervenes a vertical fold of conjunctiva, the *plica semilunaris* (fig. 322,

Ps), which rests on the eyeball; whilst, occupying the recess of the angle at the border of this fold, is a spongy-looking reddish elevation (*caruncula lachrymalis, Car*) formed by a small insulated portion of skin containing a few large modified sweat glands, as well as a group of sebaceous glands which open into the follicles of very fine hairs. There is further found in it a small amount of plain muscular tissue (H. Müller), as well as a few cross-striated muscular fibres. A few plain muscular fibres are also to be found in the plica semilunaris.

Fig. 323.

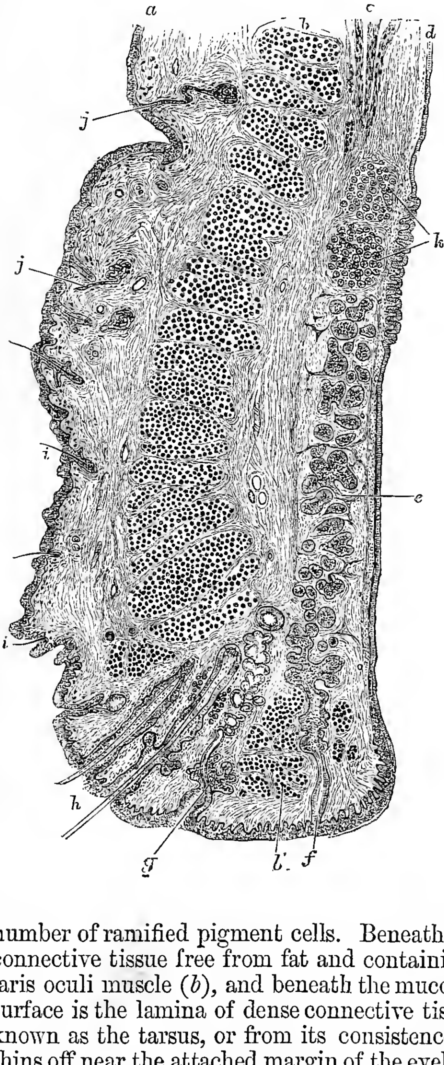


Fig. 323.—Vertical section through the upper eyelid, human (after Waldeyer). Magnified.

a, skin; *b*, orbicularis; *b'*, ciliary bundle; *c*, involuntary muscle of eyelid; *d*, conjunctiva; *e*, tarsus; *f*, Meibomian gland; *g*, sebaceous gland near eyelashes, with modified sweat-gland opening with it; *h*, eyelashes; *i*, small hairs in outer skin; *j*, sweat glands; *k*, posterior tarsal glands.

The plica semilunaris is the rudiment of the third eyelid (membrana nictitans) found in many animals; and in some animals, and occasionally in man, the caruncula lachrymalis retains its connection with the skin at the inner canthus.

Structure of the lids.—The skin covering the eyelids is thin and delicate, and covered with fine downy hairs (fig. 323, *i, i*); at the line of the eyelashes it joins the conjunctival mucous membrane which lines the inner surface of the lids. The cutis vera contains a number of ramified pigment cells. Beneath the skin is a quantity of loose connective tissue free from fat and containing the fasciculi of the orbicularis oculi muscle (*b*), and beneath the mucous membrane on the posterior surface is the lamina of dense connective tissue before mentioned (*e*), and known as the tarsus, or from its consistence, the tarsal cartilage, which thins off near the attached margin of the eyelid into the palpebral ligament connecting it with the margin of the orbit. In the tarsi are imbedded the Meibomian glands (*f*). In the upper eyelid there is, in addition, the insertion of the levator palpebræ superioris, in the form of a

fibrous expansion attached to the upper or anterior surface of the tarsus.

The *orbicularis muscle* is closely attached to the skin by connective tissue, but glides loosely on the tarsal cartilages. A marginal fasciculus lies within the line of the eyelashes, separated by the bulbs of the lashes from the other fibres, and constituting the *ciliary bundle* (*b′*). The fibres of the orbicularis are very small. Its attachments have already been described in vol. I.

The *tarsi* (*tarsal cartilages*) are two thin elongated plates formed of dense connective tissue, without, according to most observers, any intermixture of cartilage-cells. They are placed one in each lid, to which they give shape and firmness. The upper one, the larger, is half oval in form, being broader near the centre and narrowing towards the angles of the lids. The lower is thinner, much narrower, and more nearly of an uniform breadth throughout. Their free edge, which is straight, is thicker than any other part. At the inner canthus they are fixed to the nasal process of the superior maxillary bone by the internal tarsal slip (vol. I., p. 273); and at the outer angle are attached to the malar bone by a fibrous band termed the outer tarsal ligament.

The *palpebral ligament* is a fibrous membrane placed beneath the orbicularis muscle, attached on the one hand to the margin of the orbit, and on the other to the tarsi, with which its tissue is continuous. The membrane is thickest at the outer part of the orbit.

On the ocular surface of each lid are seen from twenty to thirty parallel vertical rows of what look like yellow granules, lying immediately under the conjunctival mucous membrane; these are the *Meibomian glands* (fig. 324, 6, 6). They are long sebaceous glands, imbedded in the tarsi; and they open on the free margin of the lids by minute orifices, generally one for each. The glands consist of nearly straight tubes, closed at the end, with numerous small cæcal appendages projecting from the sides. The mouths of the tubes are lined by stratified epithelium continuous with that of the skin: but the ducts and the glandular recesses have a lining of cubical epithelium filled with the fatty secretion. According to Colosanti the glands have a basement membrane, and a muscular layer outside this: he further describes a network of fine nervous fibrils amongst the epithelium-cells.

Fig. 324.

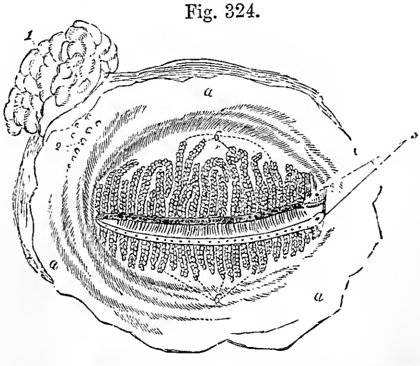


Fig. 324.—Meibomian glands of the left eyelids as seen from behind.

a, *a*, palpebral conjunctiva; 1, lachrymal gland; 2, openings of seven or eight of its ducts; 3, upper and lower puncta lachrymalia; 6, 6, ends of the upper and lower Meibomian glands, of which the openings are indicated along the margins of the eyelids.

A layer of unstriped muscular tissue is contained in each eyelid; that of the upper (fig. 323, *c*) arising from the under surface of the levator palpebræ, that of the lower from the neighbourhood of the inferior oblique muscle, and each being inserted near the attached margin of the tarsus. It may also be mentioned in

this place that H. Müller described a layer of unstriped muscle bridging over the spheno-maxillary fissure, corresponding to a more largely developed layer found in the extensive aponeurotic part of the orbital wall of various mammalia. This set of fibres has been also described by Turner (H. Müller, Wurzburg Sitzungsb., 1858; Turner, Nat. Hist. Rev., 1862). These involuntary muscles are under the influence of the cervical sympathetic.

The *eyelashes* (cilia) are strong short curved hairs, arranged in two or more rows along the margin of the lids, at the line of union between the skin and the conjunctiva. The upper lashes are more numerous and longer than the lower, and are curved in an opposite direction.

Near the inner canthus the hairs are weaker and more scattered. Immediately within the eye-lashes, between them and the ciliary bundle of the orbicularis, is a row of large modified sweat-glands, which open into the mouths of large sebaceous glands (fig. 323, *g*) (not the Meibomian).

The *conjuntiva* consists of the palpebral part (conjunctiva palpebræ), with which may be included the plica semilunaris and caruncula, and of the ocular part (conjunctiva bulbi), in which may be distinguished the sclerotic and corneal portions: each of these parts presents distinctive characters. The epithelium of the conjunctiva varies somewhat at different parts, but is mainly columnar, with smaller cells between the fixed ends of the columnar cells. Near the skin and cornea it shades off into the stratified epithelium which covers these parts.

The *palpebral portion* of the conjunctiva is thicker and more vascular than the rest of the membrane, and is freely supplied with nerves. Through the puncta lachrymalia and canaliculi, it is continuous with the lining membrane of the lachrymal sac. Although closely united to the tarsi, it exhibits, nevertheless, numerous small creases or folds, which are visible with a lens. A layer of small racemose or tubulo-racemose glands is found on the ocular surface of the lids, immediately under the conjunctiva, and beyond the blind ends of the Meibomian glands (fig. 323, *k*). Their minute ducts open near the line of reflection of the conjunctiva upon the globe of the eye.

The *ocular portion*.—The conjunctiva changes its character at the line of reflection from the eyelids, becoming thinner and being loosely connected to the sclerotic coat of the eyeball by submucous tissue. But over the cornea it consists only of a prolongation of the epithelium, which is closely adherent to the anterior layers of the cornea, in connection with which it will be described.

Vessels and nerves.—Only a few of the larger blood-vessels are generally visible in the conjunctiva in the healthy condition, but in the condition of inflammatory congestion a copious network of vessels very irregularly disposed. comes into view. These are derived from the *palpebral* and *lachrymal arteries*. Around the circumference of the cornea, they form a circle of anastomotic capillary loops. In the fœtus this plexus of vessels extends farther inwards.

Another set of vessels exists on the surface of the sclerotic, and these are also seen when congested. They are entirely sub-conjunctival and adherent to the sclerotic coat; they are less tortuous than the conjunctival set, and are derived from the anterior ciliary branches of the ophthalmic artery: they remain immovable on pressure of the eyelid, whereas the conjunctival vessels of course shift with that membrane. These sclerotic vessels dip in at the margin of the cornea, and appear to unite with a deeper minute network disposed in closely set straight lines, which radiate from the margin of the cornea.

A well developed network of *lymphatics* exists throughout the sclerotic and palpebral portions of the conjunctiva; but at the margin of the cornea a sudden diminution takes place in the size of the meshes and diameter of the vessels, which become irregular and pointed, and come into connection with ramified cell-spaces in the cornea.

Many of the *nerves* in the conjunctiva, as far as the cornea, terminate, as was shown by Krause, in end-bulbs. These have already been sufficiently described (p. 170.)

The mucous membrane of the conjunctiva contains a large quantity of lymphoid tissue, especially at its back part. Lymphoid nodules are also occasionally present, but seldom in man.

THE LACHRYMAL APPARATUS.

The parts which constitute the lachrymal apparatus are the following, viz. :—The gland by which the tears are secreted; the two canals which collect the fluid near the inner canthus, and the sac with the nasal duct continued from it, through which the tears pass into the inferior meatus of the nose.

The **lachrymal gland** (fig. 324, 1), an oblong flattened body, about the size of a small almond, is placed in the upper and outer part of the orbit, a little behind the anterior margin. The upper convex surface of the gland is lodged in a slight depression in the orbital plate of the frontal bone, to the periosteum of which it is united by fibrous bands; the lower surface is adapted to the convexity of the eye-ball, and is in contact with the upper and the outer recti muscles. The fore part of the gland, separated from the rest by a thin layer of fascia, and sometimes described as a distinct gland (*glandula lachrymalis inferior* of Rosenmüller), is closely adherent to the back of the upper eye-lid, and is covered on the ocular surface merely by the conjunctiva; its lobules are small and separate, with minute ducts, some opening separately, others joining the ducts from the principal gland, which are also very small. The number from both divisions of the gland seldom exceeds twelve or fourteen. After running obliquely under the mucous membrane, and separating at the same from each other, they open in a row at the fornix conjunctivæ, by separate orifices, at its upper outer part.

Fig. 325.

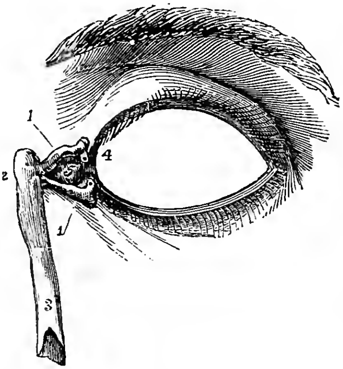


Fig. 325.—Front of the left eyelids with the lachrymal canals and nasal duct exposed.

1, 1, upper and lower lachrymal canals, showing towards the eyelids the narrow bent portions and the puncta lachrymalia; 2, lachrymal sac; 3, the lower part of the nasal duct; 4, plica semilunaris; 5, caruncula lachrymalis.

The lachrymal gland is a compound racemose gland resembling the salivary glands in general structure. Its alveoli are bounded by a basement membrane formed of ramified flattened cells; and the secreting cells exhibit changes in the different states of rest and activity of the gland similar to those seen in most

other glands (see p. 223). No rod-like structure has been noticed in the epithelium of the ducts.

Lachrymal canals.—These commence as already mentioned by a minute aperture (*punctum*) on the margin of each lid, near the inner angle (fig. 325, 1, 1). The upper canal is rather the smaller and longer of the two: it first ascends from the punctum; then makes a sudden bend, and is directed inwards and downwards to join the lachrymal sac (fig. 325, 2). The lower canal descends from the corresponding punctum and then takes a nearly horizontal course inwards. Both canals are dilated where bent. In some cases they unite near the end; more commonly they open separately, but close together, into the sac.

The **lachrymal sac** and **nasal duct** constitute together the passage by which the tears are conveyed from the lachrymal canals to the cavity of the nose. The lachrymal sac (fig. 325, 2), the slightly dilated upper portion of the passage, is situated at the side of the nose, near the inner canthus of the eye, and lies embedded in a deep groove in the ungual and superior maxillary bones. Its upper end is closed and rounded, and the lower end gradually narrows into the nasal duct. On the outer side, and a little in front, it receives the lachrymal canals; and here it is placed behind the tendo palpebrarum, and some of the inner fibres of the orbicular muscle of the lids; while on its orbital surface is the tensor tarsi muscle. The nasal duct, about half an inch or rather more in length, grooving the upper maxilla, descends to the fore part of the lower meatus of the nose, the osseous canal being completed by the ungual and lower turbinate bones. Both sac and duct are composed of fibrous and elastic tissues, adhering closely to the bones above mentioned, and strengthened in the case of the lachrymal sac by a fibrous process sent from the tendo palpebrarum, which crosses it a little above its middle. The inner surface is lined by a mucous membrane, which is continuous through the canaliculi with the conjunctiva, and through the nasal duct with the mucous membrane of the nose.

At the opening into the nose it is often arranged so as to form an imperfect valve (Hasner). The nasal duct is rather narrower in the middle than at either end; its direction is not quite vertical, but inclined slightly outwards and backwards.

The mucous membrane in the canaliculi possesses a stratified scaly epithelium, but in the nasal sac and duct a ciliated epithelium as in the nose.

THE GLOBE OF THE EYE.

The globe or ball of the eye is supported by a quantity of fat and loose connective tissue in the centre of the fore part of the orbital cavity. The recti and obliqui muscles closely surround the greater part of the eyeball, and are capable of changing its position within certain limits: the lids, with the plica semilunaris and caruncle, are in contact with its covering of conjunctiva in front; and behind it receives the thick stem of the optic nerve.

The eyeball is composed of segments of two spheres, of which the anterior is the smaller and more prominent; the segment of the larger posterior opaque sphere corresponds with the limit of the sclerotic coat, and that of the smaller sphere with the cornea.

The eyeball measures about an inch across from side to side and from above downwards, but not quite a full inch from before back.

Except when directed towards near objects, the axes of the eyes are nearly parallel ; the optic nerves, on the contrary, diverge considerably. Each nerve enters the corresponding eye about a tenth of an inch to the inner or nasal side of the axis of the eyeball.

The eyeball consists of three concentric coats, and of certain fluid and solid parts enclosed by them. The coats are (1) an external fibrous covering, forming the *sclerotic* and *cornea*, (2) a middle vascular, pigmented, and in part also muscular membrane, the *choroid* and *iris*, and (3) an internal nervous and epithelial stratum, the *retina*. The enclosed

Fig. 326.

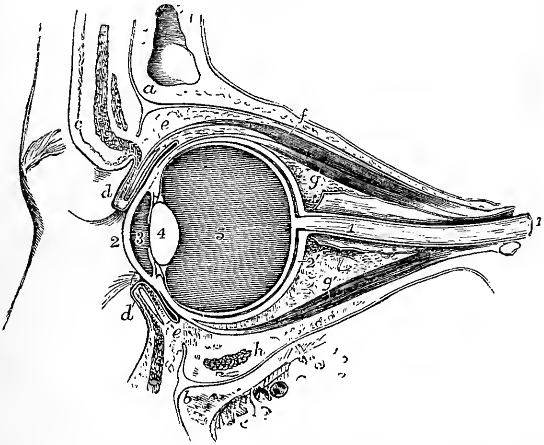


Fig. 326.—Vertical section of the left orbit and its contents. (Allen Thomson.)

The section has been carried first obliquely through the middle of the optic foramen and optic nerve as far as the back of the eyeball, and thence forward through the eyeball, eyelids, &c. *a*, frontal bone ; *b*, superior maxillary ; *c*, eyebrow ; *d*, the upper, and *d'*, the lower eyelid, partially open, showing the section of the tarsi, the eyelashes, &c. ; *e*, *e*, the reflection of the conjunctiva from the upper and lower eyelids to the surface of the eyeball ; *f*, the levator palpebræ superioris muscle ; *g*, the upper, *g'*, the lower rectus muscle ; *h*, the inferior oblique muscle divided ; 1, 1, the optic nerve divided in its sheath ; 2, the cornea ; 2', the sclerotic ; 3, aquecus chamber ; 4, crystalline lens ; 5, vitreous chamber

refracting media, three in number, are the *aqueous humour*, the *vitreous body*, and the *lens*.

Around the middle of the eyeball there is an adventitious tunic of fascia, *tunica vaginalis oculi*, or *capsule of Tenon*, which is perforated by the tendons of the recti and obliqui muscles, and connected with the sclerotic by merely the most delicate connective tissue (except posteriorly, at the entrance of the ciliary vessels and nerves, where it blends with the sclerotic). This capsule is lined by flattened epithelial cells, and encloses a lymph-space, which separates the eyeball from the orbital fat, and enables it to glide freely in its movements.

THE SCLEROTIC COAT.

The **sclerotic coat,** the tunic of the eye on which the maintenance of the form of the organ chiefly depends, is a strong, opaque,

Fig. 327

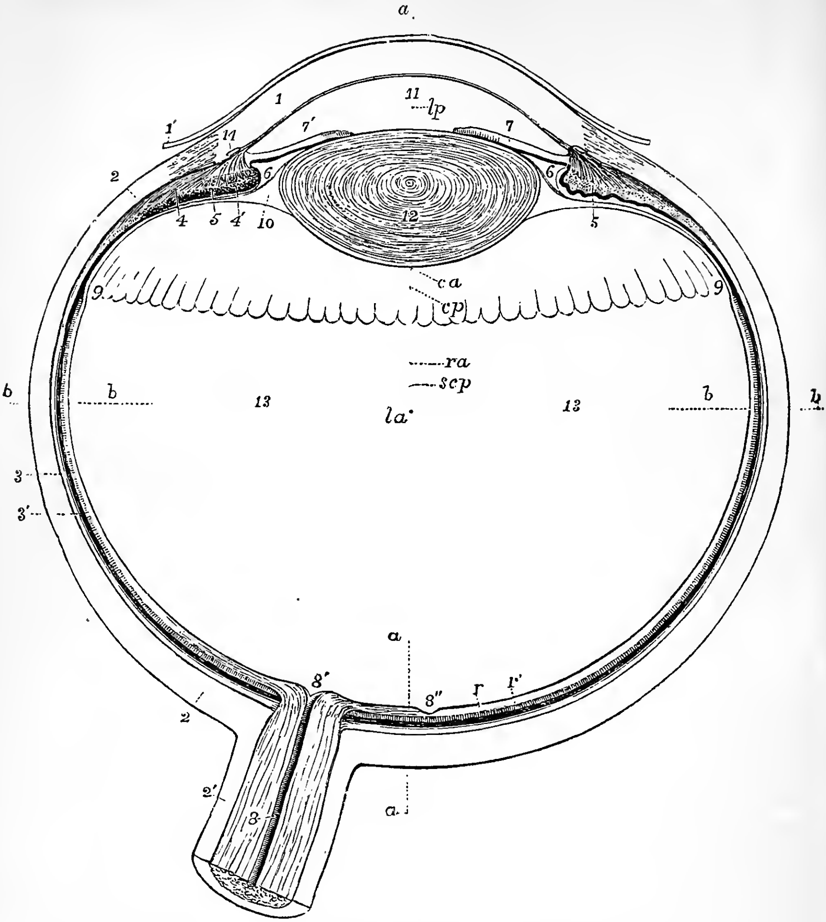


Fig. 327.—View of the lower half of the right adult human eye, divided horizontally through the middle. Magnified four times. (Allen Thomson).

The specimen from which this outline is taken was obtained by dividing the eye of a man of about forty years of age in the frozen state. It was carefully compared with other specimens obtained in a similar manner; and in the drawing averages have been given in any particulars in which differences among them presented themselves.

1, cornea; 1′, conjunctiva; 2, sclerotic; 2′, dural sheath of the optic nerve passing into the sclerotic; 3, 3′, choroid; 4, 4′, ciliary muscle; 5, ciliary process; 6, placed in the posterior division of the aqueous chamber, in front of the suspensory ligament of the lens; 7, 7′, the iris; 8, central artery of the retina; 8′, colliculus of the optic nerve; 8″, fovea centralis; 9, ora serrata; 10, so-called canal of Petit; 11, aqueous chamber; 12, lens; 13, vitreous humour; *a*, *a*, *a*, axis of the eye; *b*, *b*, *b*, *b*, equator. It will be observed that from the pupil being placed nearer the inner side the axis of the eyeball, *a*, *a*, does not pass exactly through the centre of the pupil; this line falls also a little to the inner side of the fovea centralis. The following letters indicate the centres of the curvatures of the different surfaces, assuming them to be nearly spherical, viz.: *c a*, of the anterior surface of the cornea; *c p*, posterior surface; *l a*, anterior surface of the lens; *l p*, posterior surface; *s c p*, posterior surface of the sclerotic; *r a*, anterior surface of the retina.

In connection with this figure the following average dimensions of the parts of the adult eye in fractions of an English inch may be stated :—

Transverse diameter of the eyeball	1·
Vertical diameter (Krause)	0·96
Antero-posterior diameter	0·96
Greatest thickness of the sclerotic, choroid, and retina together	0·08
Greatest thickness of the sclerotic posteriorly	0·05
Smallest thickness at the sides and in front	0·025
Thickness of the cornea in the centre	0·04
Distance from the middle of the posterior surface of the cornea to the front of the lens	0·1
Antero-posterior diameter of the lens	0·16
Transverse ditto	0·36
Greatest thickness of the ciliary muscle	0·04
Thickness of the iris	0·015
Length of the radius of curvature of the anterior surface of the cornea (regarding it approximately as spherical)	0·305
Radius of the posterior surface	0·275
Radius of the posterior surface of the sclerotic	0·5
Radius of curvature of the anterior surface of the lens	0·328
Radius of the posterior surface	0·24
Distance of the middle of the posterior surface of the lens from the middle of the retina	0·575
Distance between the centre of the spot of entrance of the optic nerve and the middle of the fovea centralis retinæ	0·14
Diameter of the base of the cornea	0·48
Diameter of the base of the iris transversely	0·45
Diameter of the base of the iris vertically	0·43
Diameter of the pupil	0·14

fibrous structure. It extends over about five-sixths of the eye-ball (fig. 327, 2,) joining in front with the cornea. The outer surface is white and smooth, except where the tendons of the recti and obliqui muscles are inserted into it. The inner surface is of a light brown colour, and rough from the presence of a delicate pigmented connective tissue (*membrana fusca*), which is united by fine threads with the choroid coat. These filaments traverse a lymphatic space through which branches of the ciliary vessels and nerves also pass obliquely. The sclerotic is thickest at the back part of the eye, and thinnest at about a quarter of an inch from the cornea: at the junction with the latter, it is again somewhat thickened. The optic nerve pierces this coat about one-eighth or one-tenth of an inch internal to the axis of the ball, and the opening is somewhat smaller at the inner than at the outer surface of the coat. The outer fibrous sheath of the nerve blends with the sclerotic at the margin of the aperture : in consequence of this arrangement, when the nerve is cut off close to the eye-ball, the funiculi seem to enter by a group of pores ; and to the part of the sclerotic thus perforated the name of *lamina cribrosa* is sometimes given. Around this cribrous opening are smaller apertures for vessels and nerves.

Structure of the sclerotic.—The sclerotic coat is formed of bundles of connective tissue fibres, and yields gelatine on boiling. Its white fibres are combined with fine elastic elements, and amongst them lie numerous connective tissue corpuscles lodged in cell-spaces, but not by any means so regularly arranged as in the cornea. Some of the cells are pigmented. The bundles are disposed in layers both longitudinally and transversely, the longitudinal arrangement being most marked at the sur-

faces. These layers communicate at intervals so as not to be separable for any distance.

Both externally and internally the sclerotic is covered with flattened epithelioid cells, which are reflected over the muscles, vessels, nerves, and connecting bands of tissue which pass from it to the capsule of Tenon and the choroid coat respectively. The lamina fusca resembles in structure the lamina suprachoroidea of the choroid coat.

At the back of the eye-ball, opposite the fovea centralis of the retina, the sclerotic is traversed in its thickness by a strand of fibrous tissue, which unites the laminæ as it passes through them. This fibrous strand is known as the *funiculus scleræ* (Hannover).

A few blood-vessels permeate the fibrous texture in the form of a network of capillaries with very wide meshes. In the neighbourhood of the cornea a zone of greater vascularity exists, which has been already noticed in the description of the sclerotic conjunctiva.

THE CORNEA.

The **cornea**, the transparent fore part of the external coat, admits light into the interior of the eyeball. It is nearly circular in shape, but is occasionally wider in the transverse direction, and its arc extends to about one-sixth of the circumference of the whole globe. Having a curvature of a smaller radius than the sclerotic, it projects forwards beyond the general surface of curvature of that membrane : the degree of its curve varies, however, in different persons, and at different periods of life in the same person, being more prominent in youth than in advanced age. Its thickness is in general nearly the same throughout, viz., from $\frac{1}{22}$ to $\frac{1}{32}$ of an inch, excepting towards the periphery where it becomes somewhat thicker. The posterior concave surface exceeds slightly in extent the anterior or convex, in consequence of the latter being encroached on by the superficial part of the sclerotic ; the cornea being overlapped by the sclerotic (to which however it is joined by continuity of tissue) like a watch glass by the edge of the groove into which it is received (see fig. 327).

STRUCTURE OF THE CORNEA.

The cornea may be described as consisting of three parts—a stratified epithelium in front (fig. 329, 1) continuous with the epithelium of the conjunctiva ; a middle part, substantia propria, or cornea proper (3), continuous with the sclerotic, composed of modified connective tissue ; and a homogeneous elastic lamella (4), bounding it behind, and itself covered with a simple layer of epithelium-like cells (5).

Epithelium of the Cornea.—The epithelium covering the front of the cornea is of the stratified kind (fig. 328). The lowermost cells (*c*) are columnar, with a flattened base, where they rest on the substantia propria, and a rounded apex, upon which a cell of the next layer fits. To the base of each columnar cell is attached a broad, flattened, strongly refracting process, which projects under one of the neighbouring cells (not shown in the figure). Above these columnar cells are two or three layers of polygonal cells, some of the deeper of which (the fingered cells of Cleland) have projections from their under surface which fit between the cells below. These polygonal cells present well-marked denticulations, which join one another across in the intercellular spaces which separate the cells. Quite superficially is a stratum of flattened scaly epithelium cells, which retain their nuclei.

The proper substance of the cornea is composed, as before said, of a modified form of connective tissue, all the constituents of which have very nearly the same index of refraction, so that in the perfectly fresh condition it is difficult, even with the best lenses, to make out any indications of structure. After death, however, and with the assistance of reagents, the cornea may be ascertained to consist of alternating lamellæ of fibrous tissue (about sixty in number, Bowman), the planes of which are parallel to the surfaces of the cornea. The fibres composing the lamellæ are nearly straight and have a definite direction in each layer;

Fig. 328.

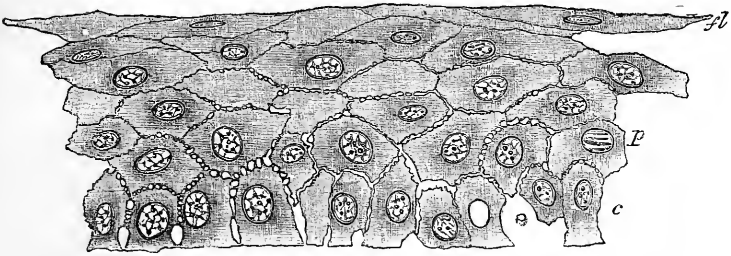


Fig. 328.—Vertical section through the epithelium of the cornea, human. (E. A. S.) Highly magnified.

c, deepest columnar cells; *p*, polygonal cells, immediately above them; *fl*, flattened cells of the surface.

The section is slightly broken on the right of the figure. The intercellular channels bridged across by processes extending from one cell to another are distinctly seen.

they cross one another at right angles in the alternate layers (fig. 329, *b*, *d*). It must, however, be understood that the latter are not individually distinct, but give off frequent offsets to the layers above and below, so that they cannot readily be stripped away for any distance. The fibrils are collected into roundish bundles, which, as well as the laminæ they form, are, as in the connective tissue elsewhere, separated from each other by ground-substance. The latter is in greater abundance between the fibrous strata than elsewhere, and in these parts the cell-spaces of the tissue are found. These cell-spaces, which are readily demonstrated by staining the tissue with nitrate of silver (fig. 331), are flattened conformably with the lamellæ, are of an irregularly stellate figure, and freely communicate by their offsets both with others on the same plane and with those above and below. The greater regularity of arrangement which characterises them, as compared with the cell-spaces of connective tissue elsewhere, is dependent on the regularly laminated structure of the cornea.

The corpuscles of the tissue—*corneal corpuscles*—lie within the cell-spaces, corresponding generally with them in form, but without entirely filling them, the room left serving for the passage of lymph and lymph-corpuscles. The protoplasm of the corpuscles is clear, except in the neighbourhood of the nucleus, where it is more granular; the cells send branching processes along the anastomosing canals of the cell-spaces, which join with those of neighbouring corpuscles. In vertical sections the corpuscles appear fusiform (fig. 329, *c*), but horizontal sections show them to be flattened conformably with the surface (fig. 330).

In the human cornea the cell-spaces can be filled with fluid injection by inserting the nozzle of a fine syringe into the tissue, and employing a very low pressure; in this way a network of anastomosing stellate figures is obtained (Recklinghausen's canals); if, however, the injection-fluid be too consistent, or if too great force be employed, the injection becomes extravasated in the interstices of the fibril-bundles, the direction of which it takes; and the appearance

Fig. 329.

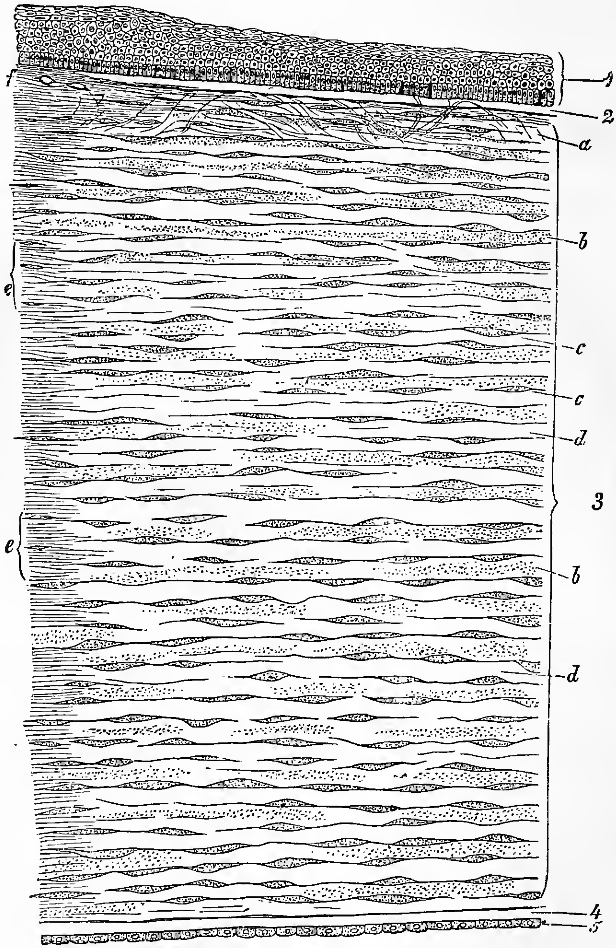


Fig. 329.—VERTICAL SECTION OF HUMAN CORNEA FROM NEAR THE MARGIN (Waldeyer). Magnified.

1, epithelium; 2, anterior homogeneous lamina; 3, substantia propria corneæ; 4, posterior homogeneous (elastic) lamina; 5, epithelium of the anterior chamber; *a*, oblique fibres in the anterior layer of the substantia propria; *b*, lamellæ the fibres of which are cut across, producing a dotted appearance; *c*, corneal corpuscles appearing fusiform in section; *d*, lamellæ the fibres of which are cut longitudinally; *e*, transition to the sclerotic, with more distinct fibrillation, and surmounted by a thicker epithelium; *f*, small blood-vessels cut across near the margin of the cornea.

is produced of minute swollen tubular passages running at right angles to one another in the different layers (Bowman's corneal tubes). This appearance may still more readily be obtained if air is injected into the tissue instead of mercury (the fluid used by Bowman), and it is seen that the injection always stops at the margin of the cornea, where the tissue becomes denser as it passes into the sclerotic, whereas Recklinghausen's canals are continued into the cell-spaces of the latter.

The part of the cornea immediately beneath the anterior epithelium, for a thickness of from $\frac{1}{2000}$ to $\frac{1}{1200}$ of an inch, is denser than the rest of the tissue, and entirely free from corpuscles (fig. 329, 2). It was named the anterior elastic lamina by Bowman, but appears not to differ materially in structure from the rest of the corneal substance, fibres from which may be seen passing obliquely towards, and becoming lost in it (fig. 329, *a*).

Fig. 330.

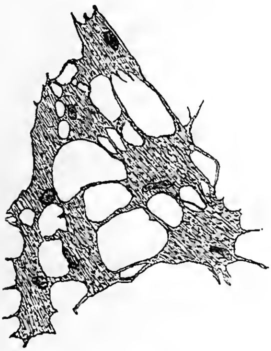


Fig. 330.—Corpuscles of the rat's cornea. From a preparation treated with chloride of gold. (E.A.S.)

Fig. 331.

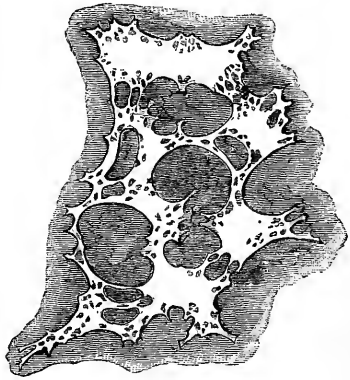


Fig. 331.—Cell-spaces of the rat's cornea. From a preparation stained with nitrate of silver. (E.A.S.)

The **membrane of Descemet or Demours** (fig. 329, 4) (posterior elastic lamina, Bowman), not very closely united with the fibrous part of the cornea, is transparent and glassy in appearance. It is firm and structureless, but very elastic ; and when shreds are removed from it they tend to curl up with the attached surface innermost. It appears not to be affected by acids, by boiling in water, or by maceration in alkalies, but under some conditions it can be split up into very fine lamellæ. In thickness it varies from $\frac{1}{3000}$ to $\frac{1}{2000}$ of an inch. It is lined next the anterior chamber with an epithelium (fig. 329, 5), which resembles that on serous membranes, consisting of a single layer of flattened polygonal cells with distinct nuclei.

At its circumference the membrane breaks up into bundles of fibres, which are partly continued into the front of the iris, forming the "pillars of the iris" and partly into the fore part of the choroid and sclerotic coats. To these festoon-like processes passing between the iris and posterior part of the cornea at its junction with the sclerotic, and which are very much more marked in the eyes of the sheep and the ox than in the

human eye, the name *ligamentum pectinatum iridis* was given by Hueck. The processes in question are covered with epithelioid cells, continued from Descemet's membrane, but these cells do not stretch across the *intervals* between the processes, so that the cavity of the aqueous chamber is prolonged into, and freely communicates with, cavernous spaces (*spaces of Fontana*) in the tissue between the processes (fig. 332, 3).

Fig. 332.

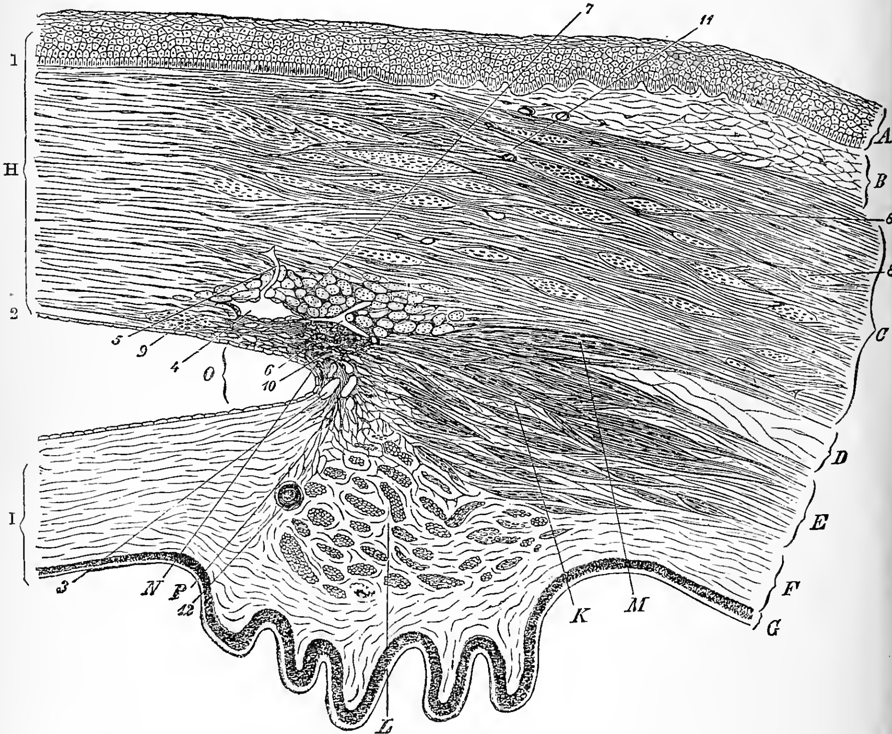


Fig. 332.—Section (from the eye of a man, aged 30), showing the relations of the cornea, sclerotic, and iris, together with the ciliary muscle, and the cavernous spaces near the angle of the anterior chamber (Waldeyer). Magnified.

A, epithelium; B, conjunctival mucous membrane; C, sclerotic; D, supra-choroid space and laminæ; E, opposite the ciliary muscle; F, choroid, with ciliary process; G, pars ciliaris retinæ; H, cornea; I, iris; K, radiating and meridional, and L, circular or annular bundles of the ciliary muscle; M, bundles passing to the sclerotic; N, ligamentum pectinatum iridis at the angle, O, of the anterior chamber; P, line of attachment of the iris; 1, anterior homogeneous lamina of the cornea; 2, posterior homogeneous lamina, covered with epithelial cells which are continued over the front of the iris; 3, cavernous spaces at the angle of the anterior chamber (spaces of Fontana); 4, canal of Schlemm, with epithelial lining, and with a vessel, 5, leading from it; 6, other vessels; 7, bundles of fibres of the sclerotic having a circular direction, cut across; 8, larger ones in the substance of the sclerotic; 9, fine bundles cut across, at limit of cornea; 10, point of origin of meridional bundles of ciliary muscle; 11, blood-vessels in sclerotic and conjunctiva, cut across; 12, section of one of the ciliary arteries.

A similar, but rather larger space is found slightly anterior to these in the substance of the sclerotic, close to its junction with the cornea. This, which is elliptical in section, is known as the *sinus circularis iridis*, or *canal of Schlemm* (fig. 332, 4).

According to Schwalbe, the canal of Schlemm communicates, through the other spaces, with the aqueous chamber of the eye. But, on the other hand, the canal of Schlemm, and the other cavernous spaces in its neighbourhood, are in communication with the *veins* of the anterior part of the sclerotic, and therefore the aqueous chamber must also through them communicate with the veins. In support of this, it was found by Schwalbe that both the spaces and the veins became filled with coloured fluid when this had been injected into the anterior chamber. Why blood does not find its way into the latter during life is not explained, since no valves have as yet been discovered in these veins or spaces : the reason given being, that greater resistance is offered to its passage here than to its return by the ordinary paths.

According to Leber on the other hand, the results obtained by Schwalbe were due to a diffusible colouring matter having been employed for filling the anterior chamber. Leber affirms that when a non-diffusible one is used it never penetrates into the canal of Schlemm, which is simply a large circular terminal vein, or a collection of two or three plexiform veins uniting at frequent intervals into one trunk. It is admitted however that fluid may pass with extreme readiness from the anterior chamber into these veins.

Vessels and nerves.—In a state of health the cornea is not provided with blood-vessels, except at the circumference, where the capillaries of the conjunctiva and sclerotic end in loops. Neither are any lymphatic vessels discoverable, unless the channels in which the nerves run, and which are lined with flattened cells and are indirectly in connection with the cell-spaces, are to be taken as representing them. The *nerves*, on the other hand, are very numerous. Derived from the ciliary nerves, they enter the fore part of the sclerotic, and are from forty to forty-five in number (Waldeyer). Continued into the fibrous part of the cornea, they retain their dark outline for $\frac{1}{20}$th to $\frac{1}{10}$th of an inch, and then, becoming transparent, ramify and form a plexus in the laminated structure, near the anterior surface. From this *primary* or *fundamental plexus* other nerves proceed, and passing obliquely through the anterior homogeneous lamina, divide into pencils of fibrils, whose general direction is towards the centre of the cornea, and which join with one another to form a much finer and closer plexus at the surface of the cornea, immediately beneath the epithelium. From this *secondary* or *subepithelial plexus* exceedingly fine, varicose, ultimate fibrils (fig. 333, *b*) pass among the epithelium-cells, and form here a third plexus or rather *network*, the *intra-epithelial* plexus, which extends almost to the free surface (fig. 333, *c*, *c*), and the fibrils of which end in minute terminal varicosities or knobs. According to Klein this does not represent the ultimate ending, but the intra-epithelial fibrils are beset with minute ramifying processes, passing off at right angles from them and forming a yet finer and closer network between the epithelium-cells.

In addition to the nerves which are destined for the epithelium, others, destined for the proper substance of the cornea, come off from the primary plexuses, and, after uniting into one or more secondary plexuses, the cords of which are still composite, eventually form, in and among the laminæ, a terminal network of ultimate fibrils, the meshes of which

are much more open than those of the intra-epithelial network (see fig. 173, *c*, *d*, p. 173). An actual connection of these nerves with the corpuscles of the cornea has never been satifactorily shown; although, since the fine nerve-fibrils run in the anastomosing cell-spaces, they come into close connection with the corpuscles and their processes, and have been described by some observers as being actually continuous with the latter.

The larger branches of the nerves are covered with a sheath of flattened cells which, as before mentioned, are in connection with the corpuscles of the cornea. At the points of junction of the plexuses

Fig. 333.

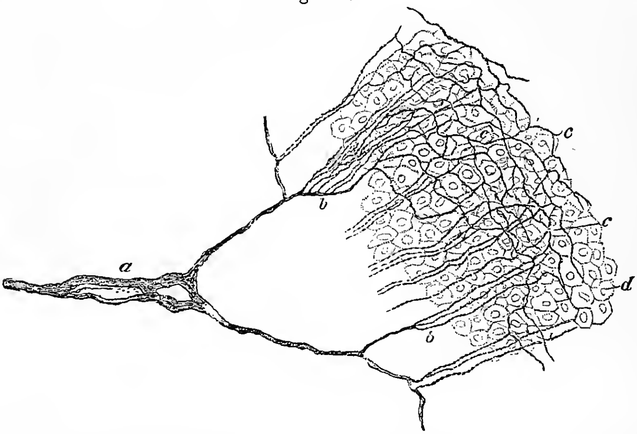


Fig. 333.—Termination of nerves in the rabbit's cornea. Chloride of gold preparation; oblique section (Klein).

a, part of the primary plexus in the substantia propria; *b*, fibrils of the secondary (subepethelial) plexus; *c*, part of the tertiary (intra-epithelial) plexus (this is represented in the figure as much closer than is actually the case).

nuclei are frequently seen, but these appear to belong to the ensheathing cells, and are not interpolated in the course of the fibres.

THE CHOROID COAT.

The **choroid coat** of the eye (tunica choroidea s. vasculosa) is a dark brown membrane lying between the sclerotic and the retina. Anteriorly it is continued into the iris, but before it passes into this it forms a number of radial inwardly projecting thickenings named ciliary processes, disposed in a circle and embedded in corresponding pits in the surface of the vitreous humour and suspensory ligament of the lens. The choroid coat is thickest behind where it is pierced by the optic nerve. The outer surface is connected to the sclerotic by loose connective tissue and by vessels and nerves which pass obliquely across a lymph-space which otherwise serves to separate the two tunics. The inner surface, which is smooth, is covered by the hexagonal pigmented cells of the retina. These, when the retina is detached, generally remain adherent to the choroid, and were formerly described as belonging to that coat,

but they are now known to be intimately related, both in their development and also physiologically, to the retina.

Fig. 334.

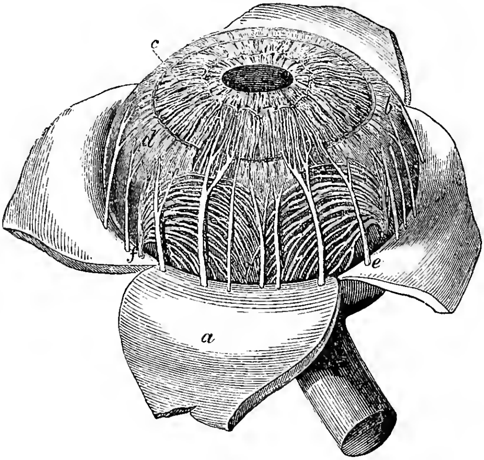


Fig. 334.—CHOROID MEMBRANE AND IRIS EXPOSED BY THE REMOVAL OF THE SCLEROTIC AND CORNEA (after Zinn). TWICE THE NATURAL SIZE.

a, part of the sclerotic thrown back; *b*, ciliary muscle; *c*, iris; *e*, one of the ciliary nerves; *f*, one of the vasa vorticosa or choroidal veins.

The *ciliary processes* (fig. 335), about seventy in number, are arranged meridionally, and together form a circle. They consist of larger and smaller thickenings without regular alternation. Each of the larger ones, measuring about $\frac{1}{10}$ of an inch in length and $\frac{1}{40}$ in depth, forms a rounded projection at its inner (anterior) end, which is free from the pigment which invests the rest of the structure; but externally they gradually taper, and disappear. The smaller processes are only half as deep as the others, and about one-third as numerous. At and near the inner ends the processes are connected by lateral projections.

Fig. 335.

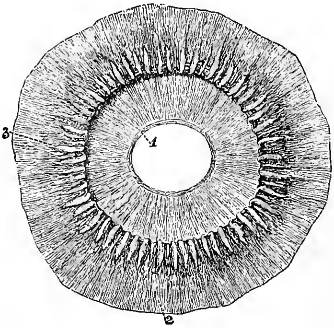


Fig. 335.—CILIARY PROCESSES AS SEEN FROM BEHIND. TWICE THE NATURAL SIZE.

1, posterior surface of the iris, with the sphincter muscle of the pupil; 2, anterior part of the choroid coat; 3, ciliary processes.

STRUCTURE OF THE CHOROID.

The choroid consists mainly of blood-vessels united by a delicate connective tissue, which contains numerous large ramified and pigmented cells.

Externally the choroid is bounded by a membranous layer similar to the *lamina fusca* of the sclerotic, and known as the *lamina suprachoroidea*. This is composed of a thin membrane (or membranes) of a homogeneous aspect, but pervaded by a network of fine elastic fibres, and covered by large flat epithelium-like cells. It contains also large flattened pigment-cells dispersed irregularly or arranged in patches, with considerable intervals free from pigment-cells; and lymphoid cells may

occur in it here and there singly or in groups (fig. 336). It is loosely united to the lamina fusca by vessels and bands of connective tissue enclosing pigment-cells, and the two laminæ as well as the uniting structures are coated with pavement-epithelium, a lymph-space being thus formed between the sclerotic and choroid. This space communicates, at the places where the vessels and nerves pierce the sclerotic, with that of the capsule of Tenon (Schwalbe).

Fig. 336.

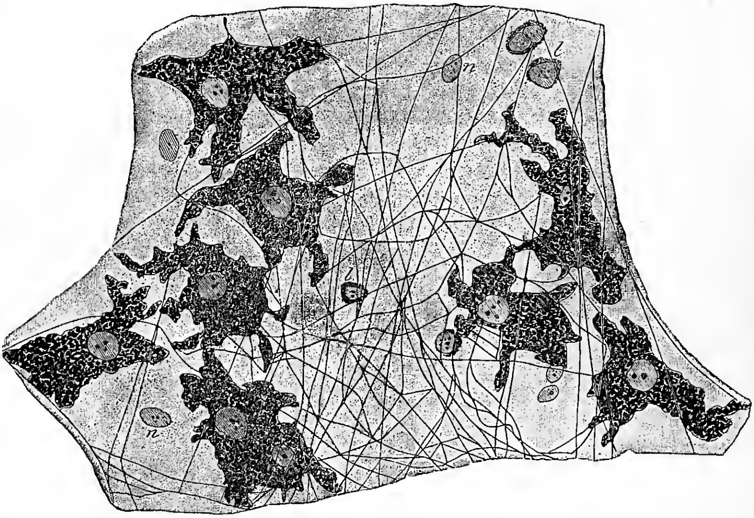


Fig. 336.—A SMALL PORTION OF LAMINA SUPRA-CHOROIDEA. Highly magnified. (E. A. S.)

p, pigment-cells; *f*, elastic fibres; *n*, nuclei of epithelioid cells (the outlines of the cells are not indicated); *l*, lymphoid cells.

The **choroid proper** resembles in general structure the lamina suprachoroidea, but contains in addition a very large number of blood-vessels. From a difference in the fineness of these constituent vessels, it resolves itself into two strata, outer and inner; the former containing the larger branches, and the latter the capillary ramifications. A layer of connective tissue which unites the two strata, and is nearly free from pigment, is sometimes described as a third or intermediate part.

In the **outer part** of the coat are situated, as just stated, the larger branches of the vessels. The arteries (*short ciliary*) are comparatively large and numerous, and piercing the sclerotic close to the optic nerve (fig. 337, *a*), divide into branches which are directed at first forwards but soon bend obliquely inwards to end in the capillary layer; whilst the veins (*vasa vorticosa*), external to the arteries, are disposed in curves as they converge to four or five principal trunks (fig. 334, *f*; figs. 337, 338, *h*) which pierce the sclerotic about half way between the margin of the cornea and the entrance of the optic nerve. In the intervals between the vessels are elongated and stellate pigment-cells.

The **inner part** of the choroid coat (*tunica Ruyschiana s. chorio-capillaris*, fig. 337, *m*) is formed mainly by the capillaries of the choroidal vessels. From the ends of the arteries the capillaries radiate (fig. 339,

3, 3), and form meshes which are closer than in almost any other texture, being especially fine at the back of the eyeball. The network reaches as far forwards as about $\frac{1}{8}$th of an inch from the cornea, or opposite the end of the retina, where its meshes become larger, and join those of the ciliary processes.

Fig. 337.

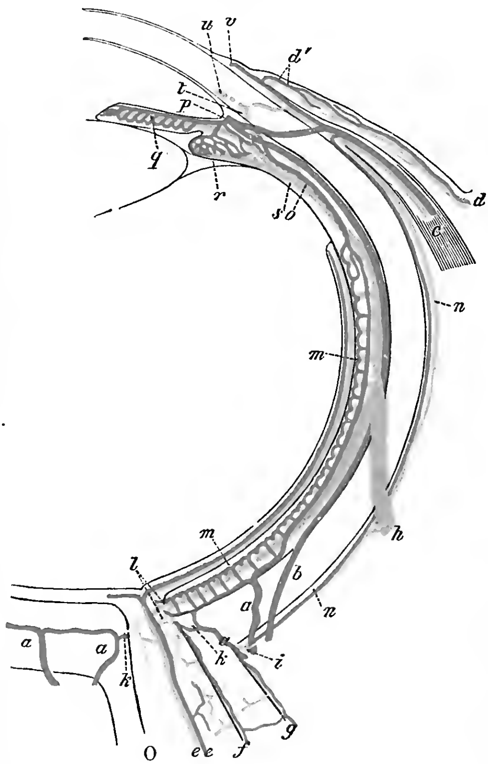


Fig. 337.—Diagrammatic representation of the course of the vessels in the eye. Horizontal section (Leber). Arteries and capillaries red; veins blue.

O, entrance of optic nerve; *a*, short posterior ciliary arteries; *a'*, branch to the optic nerve; *b*, long posterior ciliary arteries; *c*, anterior ciliary vessels; *d*, posterior conjunctival vessels; *d'*, anterior conjunctival vessels; *e*, central vessels of the retina; *f*, vessels of the inner sheath of the optic nerve; *g*, vessels of the outer sheath; *h*, vorticose vein; *i*, short posterior ciliary vein; *l*, anastomosis of choroidal vessels with those of optic nerve; *m*, choriocapillaris; *n*, episcleral vessels; *o*, recurrent artery of the choroid; *p*, circulus iridis major (in section); *q*, vessels of iris; *r*, vessels of ciliary process; *s*, branch from ciliary muscle to vorticose vein; *t*, branch from ciliary muscle to anterior ciliary vein; *u*, canal of Schlemm; *v*, capillary loop at margin of cornea.

On the inner surface of the tunica Ruyschiana is a structureless or finely fibrillated transparent membrane, the *membrane of Bruch,* which lies next to the pigmentary layer of the retina, and anteriorly, in the region of the ciliary processes, presents on its inner surface numerous microscopic reticular folds.

The **ciliary processes** have the same structure as the rest of the choroid; but the capillary plexus of the vessels is less fine, and has meshes with chiefly a longitudinal direction; and the ramified cells, fewer in number, are devoid of pigment towards the free extremities of the folds.

The *blood-vessels* of the ciliary processes (fig. 340, *d*) are very numerous, and are derived from the anterior ciliary (fig. 337, *c*) and from those of the fore part of the choroidal membrane. Several small arterial branches enter the outer part of each ciliary process, at first running parallel to each other and communicating sparingly. As they enter the prominent folded portion, the vessels become tortuous, subdivide minutely, and inosculate frequently. Finally they form short arches or loops, and turn

backwards to pour their contents into the radicles of the veins. On the free border of the fold, one artery, larger than the rest, extends the whole length of each ciliary process, and communicates through intervening vessels with a long venous trunk which runs a similar course on the attached surface.

Ciliary muscle.—At the anterior part of the choroid, between it and the sclerotic, is a zone of plain muscular tissue, the *ciliary muscle* of

Fig. 338.

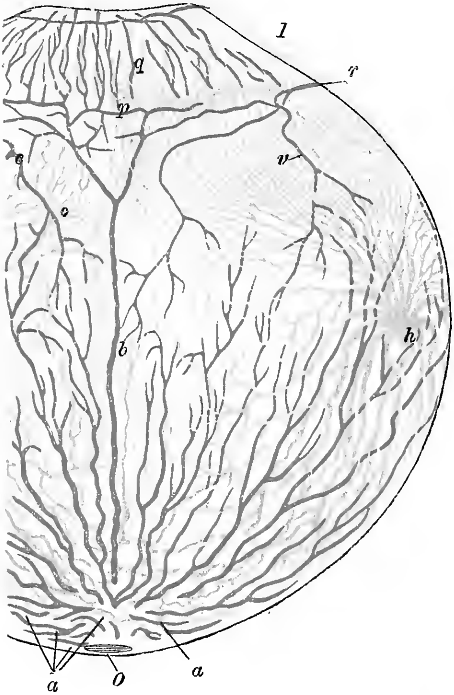


Fig. 338.—SEMI-DIAGRAMMATIC REPRESENTATION OF THE COURSE OF THE VESSELS IN THE CHOROID AND IRIS (Leber).

The ciliary muscle is supposed to be removed on the right side to show the vessels of the ciliary processes, and the converging vessels of the ciliary zone.

Bowman. It arises (fig. 332, 10) by a thin tendon from the forepart of the sclerotic close to the cornea, between the canal of Schlemm and the spaces of Fontana, and its fibres, spreading out, are directed backwards (fig. 332, K), to be inserted into the choroid opposite to the ciliary processes, and partly further back. Near their insertion the fibres pass equatorially and inter-cross so as to form peculiar stellate figures. According to Waldeyer, a small portion (the outermost) is sometimes inserted into the sclerotic coat (fig. 332, M). These antero-posterior, or *meridional and radiating fibres*, pass at the side next the iris into a ring of fibres (L), which have a circular course around the insertion of the iris. This set forms the *circular ciliary muscle* of H. Müller. This circular muscle is much developed in hypermetropic eyes, but is atrophied, or may even, it is said, be absent in myopic (Iwanoff). The ciliary muscle, at least its inner part, was formerly described as the *ciliary ligament*. In birds the ciliary muscle is composed of cross-striped muscular fibres.

The *nerves* of the choroid will be described with those of the iris.

THE IRIS.

The **iris** is the contractile and coloured membrane which is seen behind the transparent cornea, and gives the tint to the eye. In its centre it is perforated by an aperture—the *pupil*.

At its circumferential border, which is nearly circular, the iris is

continuous with the choroid, and by the ligamentum pectinatum, with the cornea: the free inner edge is the boundary of the pupil. The iris measures half an inch across, and, in a state of rest, about one-fifth of an inch from the circumference to the pupil. The anterior surface, variously coloured in different eyes, is marked by waved lines converging towards the pupil, near which they join in a series of irregular elevations; and, internal to these, other finer lines pass to the pupil. The posterior surface is covered with dark pigment, and is marked by a number of fine converging folds or thickenings prolonged from the ciliary processes.

Fig. 339.

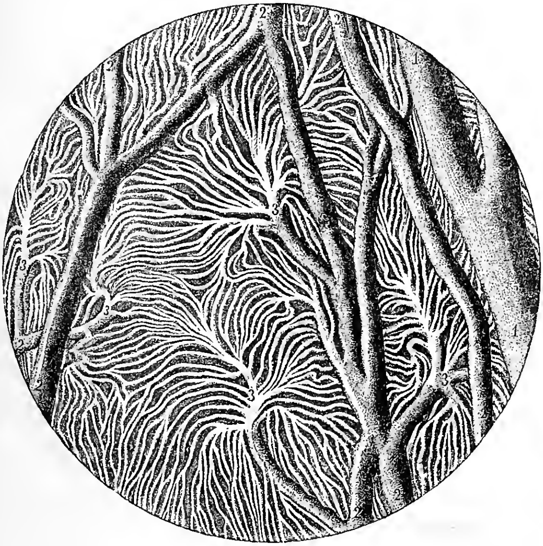


Fig. 340.

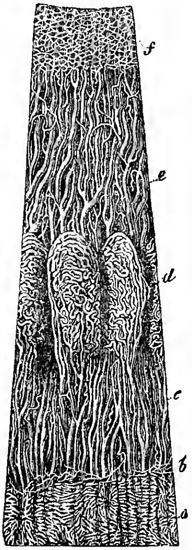


Fig. 339.—Injected blood-vessels of the choroid coat (from Sappey). 30 diameters.

1, one of the larger veins; 2, small communicating vessels; 3, branches dividing into the smallest vessels.

Fig. 340.—Vessels of the choroid, ciliary processes, and iris of a child (Arnold) Magnified 10 times.

a, capillary network of the posterior part of the choroid, ending at *b*, the ora serrata; *c*, arteries of the corona ciliaris, supplying the ciliary processes, *d*, and passing into the iris, *e*; *f*, the capillary network close to the pupillary margin of the iris.

The **pupil** is nearly circular in form, and is placed a little to the inner side of the centre of the iris. It is constantly varying in size during life, the variation ranging from $\frac{1}{20}$th to $\frac{1}{3}$rd of an inch, and regulating the quantity of light admitted to the eyeball. It is habitually wider in young than in old persons.

STRUCTURE OF THE IRIS.

A delicate connective tissue forms the framework of the iris, and pigment cells are scattered through the texture. It contains also numerous vessels and nerves. The epithelial layer of the membrane of

Descemet (fig. 332, 2) is continued from the margin of the cornea over the front of the iris; its cells are smaller and more granular than those which cover the membrane of Descemet, but are otherwise similar.

The **stroma** consists of cells and fibres of connective tissue, the latter directed for the most part radially towards the pupil.

In the substance of the iris anteriorly and throughout its thickness are variously-shaped ramified pigment cells like those in the choroid. The pigment contained in them is yellow, or of lighter or darker shades of brown, according to the colour of the eye. At the posterior surface is a covering of dark pigment, the *uvea* of authors; this is continuous with the (retinal) pigmentary layer lining the ciliary processes, and here consists of several strata of small roundish cells filled with black pigment-granules. The colour of the iris depends on the pigment in the stroma-cells; in the different shades of blue eye it arises from the black pigment of the posterior surface appearing more or less through the stroma, which in such cases is only slightly coloured or is colourless; but in the black, brown, and grey eye, the colour is due to the pigment-cells scattered through the substance of the stroma itself.

The **muscular tissue** is of the non-striated kind, and is disposed as a ring (*sphincter*) around the pupil, and as rays (*dilatator*) from the sphincter to the circumference.

The *sphincter* (fig. 341, *a*) is a narrow band about $\frac{1}{40}$ of an inch wide, situated close to the pupil posteriorly. Near the margin of the pupil the fibres are close together, but the outermost fibres are more separated, and form less complete rings.

Fig. 341.

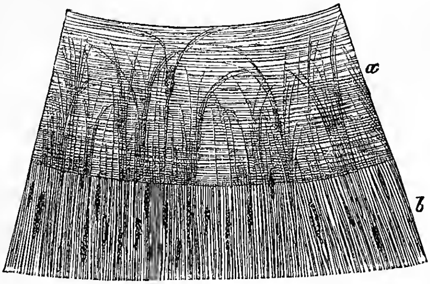


Fig. 341.—Segment of the iris, seen from the posterior surface after removal of the uveal pigment (Iwanoff).

a, sphincter muscle; *b*, dilatator muscle of the pupil.

The *dilatator* (*b*), less apparent than the sphincter, begins at the ciliary or outer margin of the iris, and its fibres, forming a continuous membrane close to the posterior surface, converge towards the pupil. Here they bend round and blend with the sphincter, some reaching nearly to its inner margin. At their origin at the ciliary margin, they also arch round and take a somewhat circular direction.

Vessels of the iris.—The *long ciliary arteries*, two in number, pierce the sclerotic a little in advance, and one on each side, of the optic nerve. Having gained the interval between the sclerotic and choroid coats, they extend horizontally forwards (figs. 337, 338, *b*, fig. 342, 1) covered by loose connective tissue to the ciliary muscle. In this course they lie nearly in the horizontal plane of the axis of the eye-ball, the outer vessel being however a little above, and the inner one a little below the level of that line. A little behind the attached margin of the iris, each vessel divides into an upper and a lower branch, and these, anastomosing with the corresponding vessels on the opposite side and with the anterior ciliary, form a vascular ring (*circulus major*, fig. 338, *p*, fig. 342, 3) in this

situation. From this circle small branches arise to supply the ciliary muscle; whilst others converge towards the pupil, and there, freely communicating by transverse offsets from one to another, form a second circle of anastomosis (*circulus minor*), from which capillaries are continued inwardly and end in small veins.

The *anterior ciliary arteries* (fig. 337, *c*, fig. 342, 2, 2), five or six in number, but smaller than the vessels just described, are supplied from the muscular and lachrymal branches of the ophthalmic artery, and pierce the sclerotic about $\frac{1}{12}$th of an inch behind the margin of the cornea; they divide into branches which supply the ciliary processes, and join the circulus major.

Fig. 342.

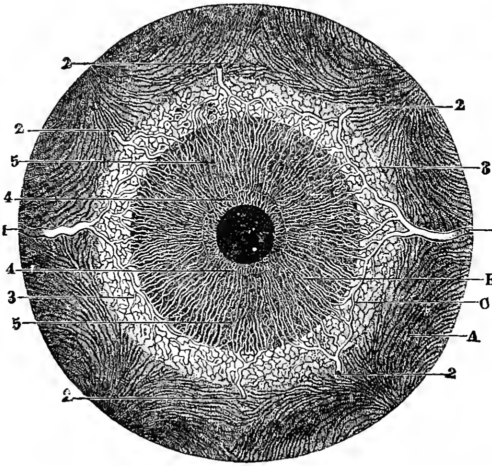


Fig. 342.—Front view of the blood-vessels of the choroid coat and iris from before (Arnold). Magnified $2\frac{1}{2}$ times.

A, choroid; B, iris; C, ciliary muscle; 1, 1, long ciliary arteries; 2, 2, five of the anterior ciliary arteries ramifying at the outer margin of the iris; 3, loop of communication between one of the anterior and one of the long ciliary arteries; 4, internal circle and network of the vessels of the iris; 5, external radial network of vessels.

Besides these special arteries, numerous minute vessels enter the iris from the ciliary processes.

The *veins of the iris* follow closely the arrangement of the arteries just described. The canal of Schlemm communicates with this system of vessels.

Nerves of the choroid and iris.—The *ciliary nerves* (fig. 334), about fifteen in number, and derived from the lenticular ganglion and the nasal branch of the ophthalmic division of the fifth nerve, pierce the sclerotic near the entrance of the optic nerve, and come immediately into contact with the choroid. They are somewhat flattened in form, are partly embedded in grooves on the inner surface of the sclerotic, and communicate occasionally with each other before supplying the cornea and entering the ciliary muscle. When the sclerotic is carefully separated from the subjacent structures, these nerves are seen lying on the surface of the choroid, into which they send branches, and in which they form a gangliated plexus amongst the blood-vessels, the groups of ganglion-cells being often applied to the walls of the vessels. Within the ciliary muscle the nerves also subdivide minutely, forming here another plexus, which contains a number of medullated fibres, and the cells of which are smaller. A few recurrent branches appear to pass back from it into the choroid coat, but the greater number pass on to the iris (fig. 343, *a*, *a*). In the iris the nerves follow the course of the blood-vessels, dividing into branches, which communicate with one another as far as the pupil,

forming a close plexus of fine non-medullated fibres. Their ultimate destination is probably the muscular tissue of the iris and of its vessels.

Fig. 343.

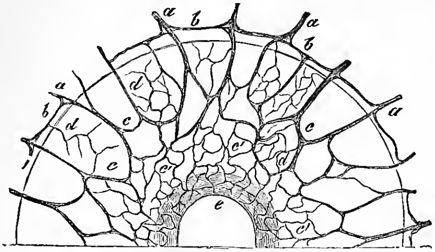


Fig. 343. — Distribution of nerves in the iris (Kölliker). 50 Diameters.

The preparation was from the eye of an albino rabbit; *a*, smaller branches of the ciliary nerves advancing from the choroid; *b*, loops of union between them at the margin of the iris; *c*, arches of union in the iris; *c'*, finer network in the inner part; *e*, sphincter pupillæ muscle.

THE RETINA.

The retina is a delicate membrane, which contains the expanded termination of the optic nerve. It lies within the choroid coat, and rests on the hyoloid membrane of the vitreous humour. It extends forwards nearly to the outer edge of the ciliary processes of the choroid, where it ends in an indented border, named *ora serrata*. From this border there is continued onwards a thin layer of a different structure and containing no nerve-fibres, the *pars ciliaris retinæ*, which reaches as far as the tips of the ciliary processes, and there gives place to the uveal pigment, which is continued on to the posterior surface of the iris. The thickness of the retina diminishes from behind forwards, from $\frac{1}{50}$th to $\frac{1}{200}$th of an inch. In the fresh eye it is translucent and of a light pink colour, but of a purple-red colour if carefully shaded from the light for a little while before removal. Under the influence of sunlight however it is quickly bleached and after death it soon becomes opaque. Its outer surface is covered with a layer of hexagonal pigment-cells which, as the study of the development of the parts shows, must be regarded as belonging to the retina and not to the choroid, to which it has usually been ascribed. Moreover the pigment-cells send fine offsets

Fig. 344.

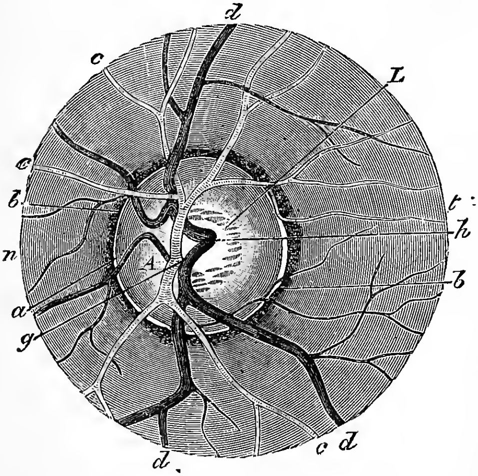


Fig. 344. — The back of the retina with the point of entrance of the optic nerve as seen with the ophthalmoscope (E. Jaeger).

A, optic nerve, passing through the lamina cribrosa, L, which shows through the disk-like expansion of the entering nerve; *a*, ring of connective tissue; *b*, choroidal ring; *c*, branches of the central artery of the retina, *g*; *d*, branches of the central vein, *h*; *n*, inner or nasal side; *t*, outer or temporal side.

between the external retinal elements. When the choroid is detached these offsets are ruptured and the pigmentary layer comes away with it. The inner surface of the retina is smooth: on it the following objects may be seen. In the axis of the ball is a yellow spot—*macula lutea* (*limbus luteus*, Sömmerring)—which is somewhat elliptical in shape (fig. 347, *b*), and about $\frac{1}{20}$th of an inch in diameter: in the centre of this, again, is a slight hollow, *fovea centralis*, and, as the retina is thinner here than elsewhere, the pigmentary layer is clearly visible through it, giving rise to an appearance as of a hole through the tunic. About $\frac{1}{10}$th of an inch

Fig. 345.

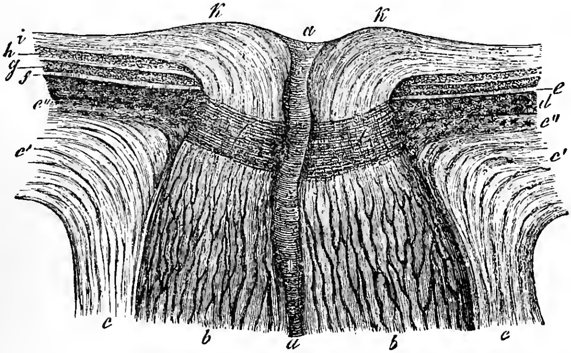


Fig. 345.—SECTION THROUGH THE MIDDLE OF THE OPTIC NERVE AND THE TUNICS OF THE EYE AT THE PLACE OF ITS PASSAGE THROUGH THEM (altered from Ecker). $\frac{6}{1}$

a, arteria centralis retinæ; *b*, fasciculi of optic nerve fibres; *c*, dural sheath of the optic nerve, passing into *c'*, the sclerotic coat; *c''*, membrana fusca; *d*, choroid; *e*,*f*, layer of rods and cones; *g*, the nuclear layers; *h*, layer of nerve-cells; *i*, layer of nerve-fibres; *k*, colliculus or eminence at the entrance of the optic nerve; *l*, lamina cribrosa.

inside the yellow spot is the round disc, *porus opticus* (fig. 344, A; fig. 347, *a*), where the optic nerve pierces the retina and expands to form its inner layer. At this place the nervous substance is slightly elevated so as to form an eminence (*colliculus nervi optici*) (fig. 345, K, K), and in its centre is the point from which the vessels of the retina branch.

When examined during life by the aid of the ophthalmoscope, the optic disc appears of a light grey tint, contrasting strongly with the colour of the rest of the field (see fig. 344).

MICROSCOPIC STRUCTURE OF THE RETINA.

When vertical sections of the retina, *i.e.*, sections made perpendicularly to its surface, are submitted to microscopic examination, eight distinct strata are recognizable, together with certain fibrous structures which pass vertically through the membrane and connect the several layers.

The following are the designations of the layers, from within outwards

1. The layer of nerve-fibres (nerve-layer).
2. The layer of nerve-cells (ganglionic layer).
3. The inner molecular layer.
4. The inner nuclear layer.

5. The outer molecular layer (internuclear).
6. The outer nuclear layer.
7. The layer of rods and cones (columnar layer).
8. The layer of hexagonal pigment cells (pigmentary layer).

Fig. 346.

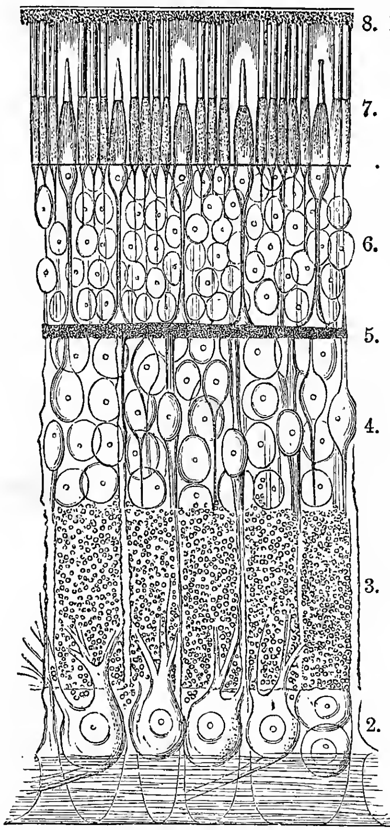


Fig. 346.—DIAGRAMMATIC SECTION OF THE HUMAN RETINA (Schultze).

In addition to these eight strata two very delicate membranes are described—the one, *membrana limitans interna*, bounding the retina on its inner surface, next to the hyaloid membrane of the vitreous humour; the other, *membrana limitans externa*, lying between the outer nuclear layer and the layer of rods and cones; but, as will be afterwards explained, these so-called "membranes" are merely the boundary lines of the sustentacular tissue of the retina. The accompanying figure, from Max Schultze, represents (somewhat diagrammatically) the general arrangement and structure of the layers. The several layers of the retina will first be considered successively as they are met with from

within out, after which the sustentacular fibres or fibres of Müller which traverse several of the layers will be described, and finally an account will be given of those parts of the retina which present points of difference from the rest, especially the central fovea, and the ciliary part.

1. **Layer of nerve-fibres.**—The optic nerve (fig. 345, *b b*) passes at the porus opticus directly through the thickness of the retina to reach its inner surface, on which it spreads out in the form of a membrane (fig. 347) which extends to the ora serrata. Its fibres, which are destitute of a primitive sheath and vary much in size but are mostly small, lose their medullary sheath on reaching the retina, consisting there of axis-cylinder only (Bowman). They are collected into small bundles, which, compressed laterally, intercommunicate and form a delicate web with narrow elongated meshes. At the yellow spot this layer is almost wanting (fig. 347, *b*), but elsewhere it forms a continuous stratum, gradually diminishing in thickness in front, interrupted only by the enlarged ends of the fibres of Müller to be afterwards described (fig. 346, 1). The nerve-bundles, as well as the cells of the next layer,

Fig. 347.

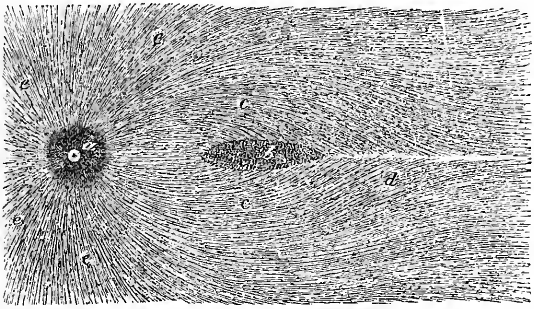


Fig. 347.—Part of the layer of nerve-fibres on the inner surface of the retina (Kolliker). Magnified.

a, colliculus opticus; *b*, yellow spot; *c*, *d*, bundles of nerve-fibres passing round this; *e*, *e*, bundles radiating in all directions from the point of entrance of the nerve.

are partially covered and supported by flattened cells like those met with in the interstitial tissue of the nervous centres and probably belonging to the connective tissue.

2. **Ganglionic layer.**—Immediately external to the nerve-fibre layer is a stratum of nerve-cells (fig. 346, 2), of a spheroidal or pyriform figure, and having in the fresh condition a pellucid aspect. Each cell has a single unbranched process extending obliquely from its rounded inner extremity amongst the fibres of the preceding layer, with one of which it is no doubt continuous. From the opposite end of the cell, which is frequently imbedded in the granular substance of the succeeding layer, one or more much thicker processes extend outwards for a variable distance into that stratum, and after branching dichotomously once or twice become lost in its substance. The number of nerve-cells and consequently the thickness of the ganglionic layer in the different regions of the retina varies exceedingly. Over the greater part of the retina they form a single stratum, but in the neighbourhood of the

yellow spot they are placed two or three deep. At the spot itself (fig. 355, 2) they are very thickly set (from eight to ten deep); the cells are also much smaller here, and are bipolar. Towards the ora serrata, on the other hand, there is but a single stratum, and that frequently incomplete.

3. **Inner molecular layer.**—Next in order to the ganglionic layer comes a comparatively thick stratum of a granular-looking substance, which in the hardened retina exhibits, under high powers of the microscope, the appearance of a network or spongework of fine homogeneous trabeculæ with reticulated interstices, occupied probably by lymph (Retzius). The substance presents both in the fresh and hardened condition a considerable resistance to the action of chemical re-agents. The fibres of Müller pass through this layer without being directly connected with its substance; the offsets of the ganglion-cells can also be traced into it for a greater or less distance; and, lastly, the fine, varicose central processes of the nuclear bodies of the layer next to be described can be followed a short distance into it (fig. 350), passing in the direction of the ganglionic and nervous layers. Flattened cells, similar to those noticed in the nerve-fibre and ganglionic layers, are also said to occur in the inner molecular layer, especially on its surfaces (Golgi and Manfredi).

4. **Inner nuclear layer.**—This is mainly composed of a number of characteristic transparent nucleus-like bodies, which are frequently known collectively as the "inner granules," but are of three or four distinct kinds. Those of the *first* kind, by far the most numerous (fig. 350,4), are round or oval clear bipolar cells, prolonged at either end into a delicate fibre, the cell being almost entirely occupied by a nucleus of corresponding shape, with a distinct nucleolus. These last (the nucleus and nucleolus) resemble very closely the analogous structures found in ganglion-cells, and indeed the bodies in question are commonly regarded as nerve-cells, but with the protoplasm of the cell very small in amount, devoid of granules, and principally collected at either end of the nucleus.

Of the processes or fibres which proceed from these cells, the inner one, or that extending into the inner molecular layer towards the ganglionic and nerve-fibre layers, is finer than the other, is always unbranched, and generally exhibits minute varicosities similar to those on the ultimate fibrils of the nerves. A direct connection of these inner processes with the outwardly extending branches of the large nerve-cells of the ganglionic layer has not been completely substantiated; but it is considered probable that some of them may be so connected, while others may pass directly to the nerve-layer and there become continued into a nerve-fibre. The outer prolongation or process of the bipolar cell is not varicose, is thicker than the inner one, and in some cases passes undivided into the next layer, in others divides into branches either in this or before reaching it. The further destination of this process will be afterwards referred to.

The relative length of the inner and outer process naturally differs according to the position of the individual cell in the nuclear layer; if the cell is near the inner molecular layer the outer process will have a longer course to reach the outer molecular layer, and, conversely, if the cell is near the latter; in almost all cases, however, the inner process is the longer of the two, extending, as before mentioned, for some distance into the contiguous molecular layer. At the macula lutea these processes or fibres of the inner nuclear layer have a

markedly oblique direction, in other parts of the retina they run vertically towards the surfaces.

The *second* kind of "inner granule" is entirely different from those just described. The cells are devoid of processes, and are more protoplasmic; they are exclusively collected at the innermost part of the inner nuclear layer, where in man they form a nearly complete stratum (Vintschgau), and they perhaps bear some relationship to the inner molecular layer, but further investigations are required as to their nature. The same remark will apply to certain other cells which constitute a *third* well-marked variety of the inner granules, and which occur here and there in the *outermost* part of the layer. They are distinguished from the ordinary "inner granules" by their rounded form and larger size, and also, according to W. Krause, in possessing only one process—an inner one—which he regards as a terminal nerve-fibre.

Finally the fibres of Müller, as they traverse this layer, are connected with oval nuclei which more especially belong to those fibres and will be described with them.

5. **Outer molecular layer.**—The outer molecular layer is much thinner than the inner, but otherwise presents, in vertical sections of hardened retina, a similar granular appearance, with a few scattered nuclei in its substance, and in which, in the human retina and in that of most mammals, it is difficult to make out any definite structure. In the horse's retina, however, as Rivolta and others have shown, it is possible in properly prepared and isolated portions of the layer to ascertain the existence within it of flattened, irregular or stellate, finely branched, delicately granular cells to which the nuclei in question belong (fig. 348). The cell-offsets, which are exceedingly fine, form by repeated branching and union a close network or feltwork throughout the layer, the substance of which is in this way formed by them. The nuclei of the cells are clear and distinct, each with a comparatively large nucleolus; the fine fibres of the network are stated by Golgi and Manfredi to exhibit varicosities like nerve-fibrils, but according to Schwalbe the varicose fibrils in all probability do not actually form part of the network, but are intercalated in its meshes. It is, therefore, uncertain whether these cells are to be regarded as of a nervous nature themselves or merely as supporting structures for the true nervous elements. There is little doubt that a similar structure exists in mammalia generally.

Fig. 348.

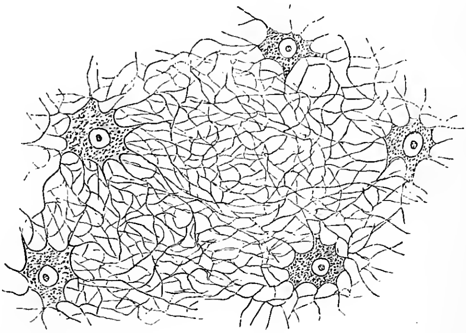


Fig. 348. — Branched cells with the uniting feltwork of fibres from the outer molecular layer of the horse's retina (Schwalbe). Highly magnified.

This layer receives the outwardly directed processes of the bipolar

inner granules, and these probably become connected within it to fibres from the rods and cones.

The layers hitherto described contain structures (cells and fibres) which are undoubtedly of nervous nature, and which appear to be developed in the same manner as corresponding structures in the brain. The two next to be described are of epithelial nature, and constitute collectively what is sometimes known as the nerve-epithelium of the retina, in contradistinction to the more strictly nervous or cerebral part. The two layers (outer nuclear and columnar) are morphologically but one, being composed of long cells, which extend through both layers. Each cell is drawn out into a fibre, and furnished with a nucleus in its inner portion, (rod- or cone-fibre and its outer granule), and is peculiarly modified both in shape and structure in its external portion (rod or cone proper).

6. **Outer nuclear layer.**—This (figs. 346, 350, 6) resembles very closely at first sight the inner nuclear layer, appearing, like that, to consist of several strata of clear, oval or elliptical, nuclear corpuscles (outer granules), from the ends of which delicate fibres are prolonged. These outer granules differ, however, essentially from the inner granules, and may be readily distinguished from them. They are of two kinds, which present well-marked differences, and are known respectively as the rod-granules and cone-granules, accordingly as they are connected with the rods or with the cones of the next retinal layer. Those which are connected with the *rods* are, in most parts of the retina, by far the more numerous, and form the main thickness of the outer nuclear layer. They may be regarded as enlargements or swellings in the course of delicate

Fig. 349.

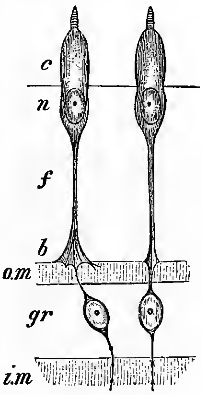


Fig. 349.—Connection of inner granules with a base of cone-fibres (after Gunn). Highly magnified.

c, cone ; *w*, cone-nucleus ; *f*, cone-fibre ; *f*, its base ; *gr*, inner granule ; *om*, outer molecular layer. The left hand figure indicates a probable connection between the base of a cone-fibre and an inner granule on the one hand ; and on the other between the same inner granule and a process of a nerve-cell *n* ; *im*, inner molecular layer.

fibres (rod-fibres), which extend from the inner ends of the rods at the membrana limitans externa through the thickness of this layer to the outer molecular layer. The enlargements, of which there is but one to a fibre, situate at any part of its course, are each occupied by an elliptical nucleus, and, in the fresh condition, exhibit a remarkable cross-striped appearance (Henle), the strongly refracting substance which mainly composes the enlargement being interrupted by bands or disks of a clearer less refracting material, usually two in number, one on each side of the middle line (fig. 350), but occasionally single and median (see the left-hand one in fig. 350). The rod-fibres are of extreme fineness, and exhibit minute varicosities in their course: each is directly continuous at the outer end with one of the rods, but at the inner end appears usually to terminate in a somewhat larger varicosity, from which one or more fine fibrils may be traced extending into the substance of the outer molecular layer.

These are probably connected with the processes of the inner granules, but the connection has not been satisfactorily proved.

Fig. 350.

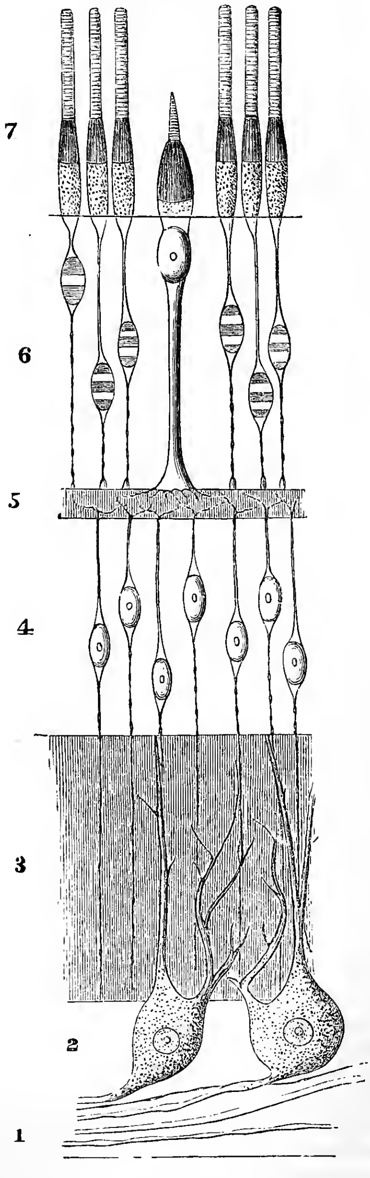


Fig. 350.—The nervous and epithelial elements of the retina (semi-diagrammatic). After Schwalbe.

The numbers are the same as in fig. 346. The extent of the molecular layers is indicated merely by linear shading.

Those outer granules which are connected with the *cones* are, in most parts of the retina, much fewer in number than the rod-granules, from which they are distinguished by their shape, which is somewhat pyriform, by the absence of transverse striation, and by their position—for they occupy the part of the outer nuclear layer nearest the membrana limitans externa, and the larger end of each is thus in close proximity to the base of the corresponding cone (fig. 349), with which it is directly connected, or there is at most a short, comparatively thick stalk uniting the two (see fig. 350). At the macula lutea, however, where only cone-granules are met with, many of them are further removed from the limiting membrane, and the stalk is then longer and more attenuated. The nucleus of each, which, as in the case of the rod-granules, occupies almost all the enlargement, contains a distinct nucleolus. The cone-fibre is very much thicker than the rod-fibre above described, and may itself appear finely striated or fibrillated. It passes from the smaller end of the pear-shaped enlargement straight through the outer nuclear layer to reach the outer molecular layer, upon which it rests by a somewhat pyramidal base, from the edges of which fine processes may be traced into the substance of the molecular layer; one at least of these processes has been shown by Gunn to be continuous with the outer or peripheral process of an inner granule (fig. 349). According to Merkel the processes abut against one another without being continuous.

7. **The layer of rods and cones.** The elements which compose this layer are, as their name implies, of two kinds, those of the one kind—the *rods*—having an elongated cylindrical form ; the *cones* on the other hand being shorter, much thicker, bulged at the inner end or base, and terminated externally by a finer tapering portion. Both rods and cones are closely set in a palisade-like manner over the whole extent of the retina between the membrana limitans externa and the pigmentary layer (fig. 346, 7). Except at the macula lutea, where only cones are met with, the rods far exceed the cones in number. Their relative number and arrangement is well exhibited when the layer is viewed from the outer surface, as in fig. 351, where *a* represents a portion of the layer from the macula lutea ; *b*, from the immediate neighbourhood of the latter ; and *c*, from the peripheral part of the retina.

Fig. 351.

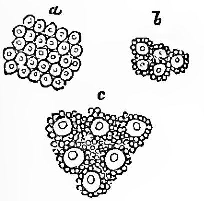


Fig. 351.—Outer surface of the columnar layer of the retina (Kölliker). 350 diameters.

a, part within the macula lutea, where only cones are present ; *b*, part near the macula, where a single row of rods intervenes between the cones ; *c*, from a part of the retina midway between the macula and the ora serrata, showing the preponderance of the rods.

Fig. 352.

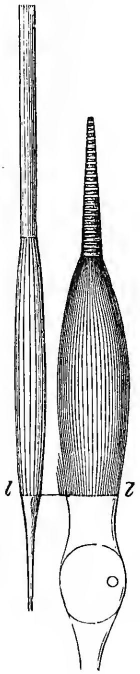


Fig. 352.—A rod and a cone from the human retina (Max Schultze). Highly magnified.

In the rod the longitudinal striation of both the outer and inner segments is shown ; in the cone the transverse striation of the outer segment and the longitudinal of the inner segment ; *l*, limitans externa.

The rods and the cones, although differing thus in shape and size, agree in many points of structure. Thus, each consists of two distinct segments — an inner and an outer ; the division between the two occurring, in the case of the rods, about the middle of their length (in man) ; in the cones at the junction of the finer tapering end-piece with the basal part ; consequently, the outer and inner segments of the rods are nearly similar in size and shape, the inner being, however, slightly bulged, whereas the inner segment of each cone far exceeds the outer one in size, the latter appearing merely as an appendage of the inner segment (fig. 352). The two segments both of the rods and cones exhibit well-marked differences, both in their chemical and optical characters, as well as in the structural appearances which may be observed in them. Thus, while in both the outer segment is doubly refracting in its action upon light, the inner is, on the contrary, singly refracting : the inner becomes stained by carmine, iodine, and other colouring fluids, whilst the outer remains uncoloured by these reagents, but is stained darkly by osmic acid. The outer segment in both shows a tendency to break up into a number of minute superimposed disks whereas the inner segment is itself again distinguishable into two parts—an outer part, composed, according to Max Schultze, of fine fibrils, and an inner part, homogeneous, or finely granular, and, at the membrana

limitans externa, directly continued into a rod or cone-fibre, the disposition of which in the outer nuclear layer has been already described.

In the **outer segments** of the *rods* there can be detected by the aid of a powerful microscope, besides a delicate transverse striation (fig. 350), corresponding to the superposed disks of which, as above mentioned, they appear composed, also fine longitudinal markings which are due to slight linear grooves by which they are marked in their whole extent. The ends of the segments are rounded and project into the pigmentary layer. The purplish-red colour of the retina before mentioned (p. 408), resides entirely in the outer segments of the rods (Boll, Kühne). A few of the rods are, however, of a green colour. The outer segments of the *cones* taper gradually to a blunt point, and do not exhibit superficial groovings, but the transverse markings are somewhat more evident than in the rods (fig. 352), although the separation into disks does not take place so readily as in the latter. This has been accounted for by supposing the existence of an extremely delicate membrane covering the whole of the outer segment of the cones. From their behaviour to staining reagents and the readiness with which they become altered after removal from the body, it has been conjectured that the substance of the inner segment is of a similar nature to the myelin of the medullary sheath of nerve-fibres.

In the **inner segments**, the proportion which the fibrillated part bears to the homogeneous basal part differs in the rods and cones. In the *rods* the fibrils usually occupy only the outer third of the inner segment (fig. 350), ceasing abruptly at its junction with the middle third; in the *cones*, on the other hand, they occupy about the outer two-thirds of the segment, only the part nearest the membrana limitans remaining free from fibrils. The fibrils in question are for the most part straight and parallel, and strongly refracting. Sometimes, in the cones, instead of this outer part of the inner segment appearing fibrillated, it appears homogeneous, but is nevertheless well marked off from the inner part by its strong refractivity. This condition of a part of the inner segment of the cones is much better marked in most of the lower vertebrata, where there occurs a distinct strongly refracting body, situated in the middle or outer part of the segment, and known from its shape as the "ellipsoid." Moreover, in these animals, the fibrils are absent from the inner segments of the rods also, a peculiar, strongly refracting, "lenticular" body being met with at their outer part, corresponding to the ellipsoid of the cones. Further, in birds, reptiles, and amphibia, there is found in the extreme outer part of the inner segment of each cone a minute globular body, apparently of a fatty nature, which in some is clear and colourless, but in many cones is brightly-coloured of a tint varying in different cones from red to green—red and yellow being the most common. Blue and violet are not met with, but by the action of iodine the colours of all become changed to blue. Sometimes the whole inner segment is found to be slightly tinted of the same colour as the "oil-globule." In all vertebrates below mammals, double- or twin-cones are here and there met with, which resemble two cones joined near their base, but separate and distinct towards their apex. Numerous other differences and peculiarities are found in animals: thus in birds the cones are more numerous than the rods; in many reptiles only cones are met with; while in some fishes (sharks and rays), in most nocturnal mammals, and in the owl, the cones are either altogether absent or are but few and rudimentary.

8. **The pigmentary layer.**—This layer, which bounds the retina externally, and was formerly described with the choroid coat, consists of a single stratum of hexagonal epithelium cells separated from one another by a perceptible amount of clear intercellular substance (fig. 353). The outer surface of each cell—that which is turned towards the choroid—is smooth and flattened, or slightly convex, and the part of the cell near this surface is devoid of pigment, and contains the nucleus; the inner boundary, on the other hand, is not well marked, for the substance of the cell, which here is loaded with pigment, is pro-

longed into fine, straight, filamentous processes (fig. 353, *b*), which extend for a certain distance between and amongst the outer segments of the rods and cones—indeed the outer parts of the rods may be said to be altogether embedded in the pigment-cells (*c*).

Fig. 353.

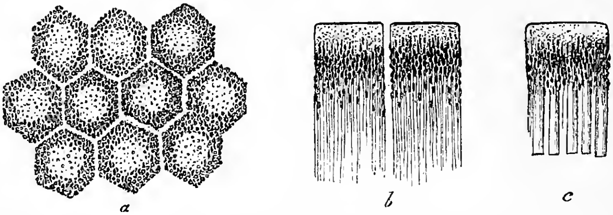


Fig. 353.—Pigmented epithelium of the human retina (Max Schultze). Highly magnified.

a, cells seen from the outer surface with clear lines of intercellular substance between; *b*, two cells seen in profile with fine offsets extending inwards; *c*, a cell still in connection with the outer ends of the rods.

The pigment granules, many of which are in the form of minute crystals, are placed for the most part, both in the cells and cell-processes, with their long axes at right angles to the surface of the retina. The distribution of the pigment granules within the cells varies during life and immediately after removal of the eye, according as the retina has been shaded from the light or exposed to its influence. In the former case the pigment is mainly accumulated in the body of the cell (or at least its inner zone), and is withdrawn to a great extent from between the rods; but after exposure to light, a large amount of pigment is found between the rods, and some of the granules may even extend as far as the external limiting membrane. The pigment appears to have the function of renewing the colour (visual purple) of the outer segments of the rods after these have become bleached from exposure to the light. This renewal of the colour will take place for a short time after the death of the animal, or the excision of the eye (Kühne).

In some animals coloured oil-droplets occur in the non-pigmented portion of the cells.

The intervals between the rods and cones are only partially filled by the processes of the hexagonal pigment-cells; the remaining part appears to be occupied by a clear substance, which, according to Henle and H. Müller, is of a soft elastic consistence during life and in the fresh condition, but soon liquefies after death; but according to Schwalbe, is normally liquid. In the embryo, between the hexagonal pigment and the remainder of the retina, there is a distinct cleft filled with fluid (remains of cavity of primary optic vesicle).

The sustentacular tissue of the retina: Müllerian or radial fibres.—In addition to the elements which belong specially to the layers above described, there are certain other structures which are common to nearly all the layers, passing through the thickness of the retina from the inner almost to the outer surface, and, if not actually of the nature of connective tissue, at least serving the same kind of purpose, namely, to bind together and support the more delicate nervous structures of the membrane. These *sustentacular fibres* or *fibres of Müller* (fig. 354), commence at the inner surface of the retina by a broad conical hollow base or foot, which is filled by granular substance, and often contains a nucleus-like body. The bases of adjoining fibres are united together at their edges, so as to give, in vertical sections of the retina, the appearance of a distinct

boundary line (fig. 346); this has been named *membrana limitans interna*, but, as may be inferred from the above description, it is in no way a continuous or independent membrane. The Müllerian fibres pass through the nerve- and ganglionic layers, either with a smooth contour, or with but two or three well-marked lateral projections from which fine lamellar processes extend amongst the elements of these layers: gradually diminishing in size they then traverse the inner molecular layer, without, according to Schwalbe, becoming actually connected with the substance which mainly composes it, although in the mammalian retina the fibres may be marked by slight projections in passing through this layer. In the inner nuclear layer they again give off delicate flattened processes from their sides, which pass round the inner granules and serve to support them. Moreover, each Müllerian fibre is here characterised by the presence of a clear oval or elliptical nucleus (already mentioned in the description of the inner nuclear layer), containing a nucleolus, and situated at one side of, and in close adherence to the fibre to which it belongs (fig. 354, *n*). On reaching the outer nuclear layer (after passing through the outer molecular) the fibres of Müller break up into fibrils and thin lamellæ, and in this form they pass outwards through the layer, between the outer granules and the rod and cone-fibres, more or less enclosing these structures, filling up the intervals between the granules and forming partial sheaths for them. At the level of the bases or central ends of the cones and rods, the numerous offsets terminate along a definite line which marks the boundary between the outer nuclear layer and the layer of rods and cones, and has been termed *membrana limitans externa*. This also, like the *m. l. interna*, is in no way a continuous membrane, nor is it isolable from the Müllerian fibres; indeed, numerous fine fibrillar offsets of these pass a short distance beyond the so-called limiting membrane, and closely invest the bases of the inner segments of the rods and cones. According to some accounts a delicate membrane prolonged from the limitans externa completely invests each cone and rod.

Fig. 354.

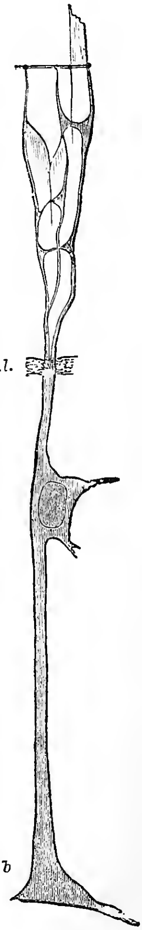


Fig. 354.—A FIBRE OF MÜLLER FROM THE HUMAN RETINA, ISOLATED (from Henle). $\frac{1000}{1}$

b, base of the fibre; *n*, its nucleus; *m.e.l*, membrana limitans externa; *e.m.l*, external molecular layer.

The Müllerian fibres exhibit a fine striation. They swell up and become indistinct on treatment with acetic acid and dilute alkalies, but much more slowly than connective tissue fibrils; moreover, they are not dissolved by boiling in water. They are much less developed in the central and posterior part of the retina than in the peripheral and anterior part; towards the ora serrata they are very distinct and closely set.

Structure of the macula lutea and fovea centralis (fig. 355).—The peculiarities in structure which these present have been for the most part incidentally noticed in the preceding description of the retinal layers. In the fovea no rods are met with, and the cones are much longer and narrower than elsewhere. All the other layers are much thinned, but towards the margin of the fovea they rapidly increase in thickness, and in the rest of the macula lutea most of them are thicker than at any other part of the retina. The ganglionic layer (fig. 355, 2) is especially thickened, the cells being from six to eight deep, bipolar and placed rather obliquely. The nerve-fibre layer (1) gradually thins towards the edge of the fovea as the fibres dip in to join the central ends of the bipolar ganglion-cells. The peripheral process of each

Fig. 355.

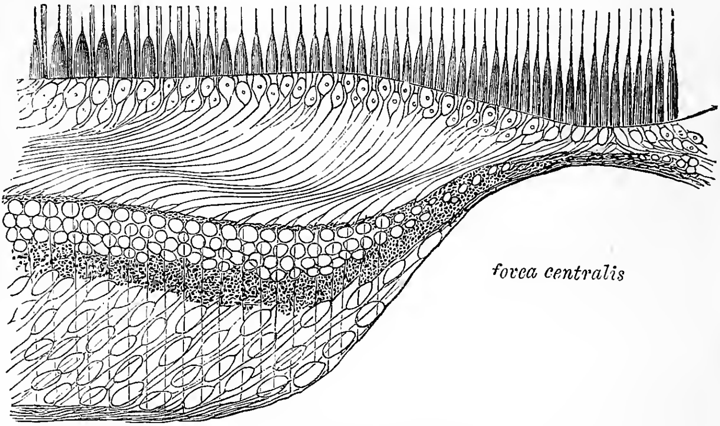


Fig. 355.—Vertical section through the macula lutea and fovea centralis; diagrammatic (after Max Schultze).

1, nerve-layer; 2, ganglionic layer; 3, inner molecular; 4, inner nuclear; and 5, outer molecular layers; 6, outer nuclear layer, the inner part with only cone-fibres forming the so-called external fibrous layer; 7, cones and rods.

ganglion-cell is said to bifurcate, each branch becoming connected with a granule of the inner nuclear layer (Merkel). The inner granules are also somewhat obliquely disposed, are large, and near the bottom of the fovea, where this layer and that of the nerve-cells run together, they can hardly be differentiated (Hulke). The outer nuclear layer (6) is occupied in the greater part of its thickness by the very long and obliquely disposed cone-fibres; the nuclei are only two or three deep, and take up a comparatively small portion of the layer.

The yellow tint of the macula is deepest towards the centre: it is due to a diffuse colouring matter which is seated in the interstices between the elements of the four or five inner layers.

Structure of the ora serrata and pars ciliaris.—At the *ora serrata* the numerous complex layers of the retina for the most part disappear, and in front of the ora serrata, the retina is represented merely by a single stratum of elongated columnar cells with the pigmentary layer external to it (*pars ciliaris*). The transition is, in man, somewhat abrupt, all the changes being met within a zone of about $\frac{1}{250}$

of an inch only in breadth. The layer of rods and cones (fig. 356, *g*) first disappears, the cones continuing rather further than the rods, but soon ceasing; the nerve- and ganglionic layers, which were already very thin and incomplete, cease altogether at the ora, the inner molecular layer (*c*), which is now largely occupied by Müllerian fibres, retains its thickness up to a certain point, and then abruptly terminates (*a'*), while the nuclear layers, outer and inner, (*f*, *d*), here become merged into a single stratum, which appears to be continuous with the columnar cells of the pars ciliaris. These cells (fig. 356, *m*), which are at first of considerable

Fig. 356.

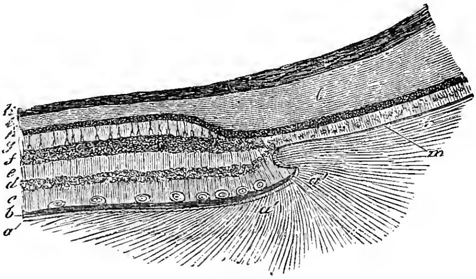


Fig. 356.—Vertical section through the choroid and retina near the ora serrata (Kölliker). 60 diameters.

a, hyaloid membrane; *b*, limiting membrane and nervous layer of the retina; *c*, ganglionic and inner molecular layers with closely set Müllerian fibres; *d*, inner nuclear; *e*, outer molecular; *f*, outer nuclear layer; *g*, columnar layer; *h*, pigment; *i*, *k*, choroid; *l*, part of one of the ciliary processes; *m*, pars ciliaris of the retina. (The recess shown at *a''* is not constant.)

length, become gradually shorter anteriorly; they are finely striated (fig. 357, 2), and each cell has a clear oval nucleus at the outer part of the cell, near the pigmentary layer. The inner end may be rounded,

Fig. 357.

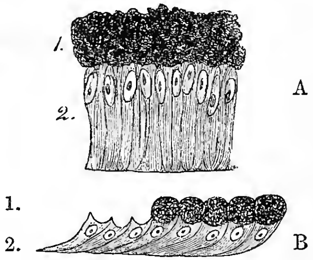


Fig. 357.—A small portion of the ciliary part of the retina (Kölliker). 350 diameters.

A, human; B, from the ox; 1, pigment-cells; 2, cells forming the pars ciliaris.

pointed, square, or even branched; the sides of the cells, too, are sometimes uneven.

These cells are considered by Kölliker to correspond with the Müllerian fibres of the retina, but according to Schwalbe the Müllerian fibres, or rather their united inner ends, are represented by a delicate membrane, which covers the inner ends of the columnar cells and sends fine offsets around and between them.

Vessels of the Retina.—A single artery (*arteria centralis retinæ*) passes between the bundles of fibres of the optic nerve to the inner surface of the retina at the middle of the papilla optici (fig. 345, *a*). It is accompanied by the corresponding vein and soon divides into branches (fig. 344), usually two, one above, the other below, each of these again dividing into two branches which arch out towards the sides; the outer ones are somewhat the larger, and as they bend round the macula lutea they send numerous fine branches into it which end at the margin of the

fovea centralis in capillary loops. The main branches of the vessels pass forwards in the nerve-fibre and ganglionic layers, dividing dichotomously as they proceed, and giving off fine offsets to the substance of the retina, where they form two capillary networks, the one in the nerve- and ganglionic layer, the other in the inner nuclear layer. The capillaries of the former are mainly connected with the arteries, and those of the latter with the veins, the communication between the two networks being effected by vertically and obliquely coursing capillaries which traverse the inner molecular layer. No vessels penetrate the outer molecular layer (His, Hesse), so that the outer retinal layers are entirely destitute of blood-vessels.

The vascular system of the retina is nowhere in direct communication with the choroidal vessels. Near the entrance of the optic nerve, however, it comes into communication with some offsets from the sclerotic coat, and the choroidal vessels also send branches to join the long-meshed network in the optic nerve furnished by the central artery. The arteries of the retina have the usual coats, but the veins resemble capillaries in structure, their walls consisting of a single layer of epithelial cells without any muscular tissue. Outside the epithelial layer is a space (perivascular lymphatic, His) both in the veins and capillaries, bounded externally by a second epithelial layer (forming the wall of the lymphatic). Outside this again is found, in the case of the veins, a layer composed of a peculiar retiform tissue. These perivascular lymphatics are in communication with the lymphatics of the optic nerve, and may be filled by injecting coloured fluid under the sheath which that nerve derives from the pia mater. Other lymph-spaces also become injected by the same process, viz., the interstices between the nerve-bundles which radiate from the papilla optici, the capillary space between the limitans interna and the hyaloid membrane of the vitreous humour, and finally even the irregular interstice between the pigmentary layer and the layer of rods and cones (Schwalbe).

THE VITREOUS BODY.

The vitreous body occupies the greater portion of the eyeball. It is quite pellucid in aspect, and of a soft gelatinous consistence. Subglobular in form, it fills about four-fifths of the ball, and serves as a support for the delicate retina, but it may be readily separated from the latter, except behind, at the entrance of the optic nerve, where the connection is closer, the retinal vessels having here entered it in fœtal life. At the fore part it is hollowed out for the reception of the lens and its capsule, to which its substance is closely adherent.

The surface of the vitreous humour is covered everywhere except in front by a thin glassy membrane, named *hyaloid*, which lies between it and the retina. No vessels enter the vitreous humour in the adult, and its nutrition must, therefore, be dependent on the surrounding vascular structures, viz., the retina and the ciliary processes.

Although in the fresh state apparently structureless, or at least presenting under the microscope but faint traces of structural elements—the so-called corpuscles of the vitreous humour to which we shall immediately recur,—yet in preparations hardened in weak chromic acid, or acted upon in certain other ways, it is possible to make out a more or less distinct lamellation of the vitreous body, especially in its peripheral part, that, namely, nearest the retina; which part in the human eye has a somewhat firmer consistence than the more central portion. From the appearances (fig. 358) which have been obtained by such modes of preparation it has been conjectured by various observers that at least in this part the vitreous substance is divided into compartments by a number of delicate membranes arranged concentrically and parallel to the surface; but the

existence of such membranous partitions has not been conclusively demonstrated. That, however, the vitreous substance does in some way consist of a firmer material—whether or not in the shape of continuous membranes—enclosing in its meshes the more fluid portion, is shown by the fact that if either the whole or a piece of the vitreous humour be thrown upon a filter, a small proportion always remains upon the latter; although by far the larger part drains away, and may be collected as a clear watery fluid.

Fig. 358.

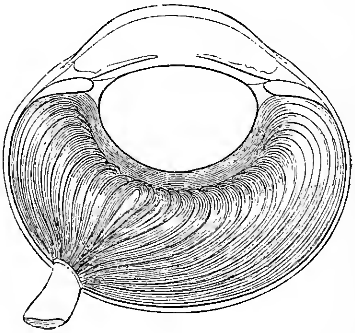


Fig. 358.—Horizontal section of the horse's eye, hardened in chromic acid (after Hannover).

The vitreous humour appears concentrically and meridionally striated throughout its whole depth.

In addition to the above-mentioned concentric striation, a radial marking has also been observed in sections of vitreous humour made transversely to the axis of the eyeball (fig. 359), but whether there is any pre-existent structure to account for the appearance is not known. It is conceivable that these appearances may be merely produced by the manner in which the albuminous substance has undergone coagulation by the reagent employed.

However this may be, there exists, nearly but not quite in the axis of the eye, a definite structure in the shape of a distinct canal, about a twelfth of an inch in diameter, filled with fluid and extending from the *papilla optici* to the back of the lens-capsule, where it apparently terminates blindly. This is the *canalis hyaloideus* or *canal of Stilling*. It is best shown in the fresh eye, and may be also injected by forcing a coloured solution under the pia-matral sheath of the optic nerve (Schwalbe). The canal widens somewhat towards its posterior part: its wall is composed of an extremely delicate homogeneous membrane. It represents the place of passage of an offset from the central artery of the retina to the capsule of the lens in the fœtus.

Fig. 359.

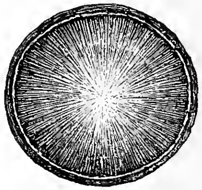


Fig. 359.—Transverse section of human eye, hardened in chromic acid, showing radial striation of the vitreous body (after Hannover).

Scattered about throughout the substance of the vitreous humour are a variable number of corpuscles, for the most part possessed of amœboid movement. Some of these cells are remarkable for the very large vacuoles which they contain, and which distend the body of the corpuscle, pushing the nucleus to one side; the cell-processes are often peculiar in possessing numerous little secondary bud-like swellings, or they may present a varicose appearance, like strings of pearls.

The hyaloid membrane invests, as before mentioned, the whole of the vitreous humour, except in front, where the membrane passes forwards to the anterior part of the margin of the lens, becoming also firmer in consistence and distinctly fibrous in structure. This portion of the hyaloid is known as the *zonula of Zinn*, or *zonula ciliaris*. It is

also known as the *suspensory ligament of the lens* (fig. 360, z). The posterior part, or hyaloid proper, is exceedingly thin and delicate, and is readily thrown into folds when detached. Under the microscope it presents no appearance of structure: but, flattened against its inner surface are generally to be seen a number of granular nucleated corpuscles, which exhibit amœboid movements: they appear to be migrated white blood corpuscles. The ciliary part or commencing zonula, on the other hand, presents radiating meridional fibres, stiff in appearance but possessed of considerable elasticity; they commence about opposite the ora serrata, and strengthen this portion of the hyaloid membrane. From the ciliary processes the zonula is continued as a distinct membrane to the front of the lens, to the capsule of which it is anteriorly firmly attached. But in addition to this anterior membranous prolongation of the hyaloid membrane, other of its fibres, more scattered in their disposition, pass across to the periphery of the lens, some being attached to the extreme edge, others passing into continuity with the posterior capsule, and others again occupying intermediate positions (fig. 360, *P*). The interstices of these *suspensory fibres of the lens* are occupied during life by fluid, or perhaps in part by

Fig. 360.

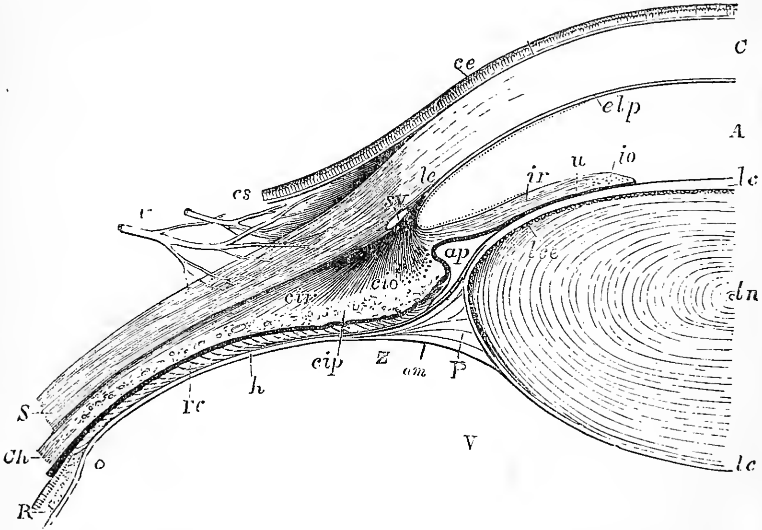


Fig. 360.—Sectional view of the connections of the cornea, sclerotic, iris, ciliary muscle, ciliary processes, hyaloid membrane and lens (Allen Thomson). $\frac{8}{1}$

The specimen extends from the middle of the lens to the ora serrata on the inner side of the right eye. *C*, cornea; *cs*, conjunctiva; *ce*, epithelium of the cornea; *elp*, posterior elastic layer; below *le*, ligamentum pectinatum iridis; *S*, sclerotic; *A*, the aqueous chamber; *ap*, the recess forming the posterior division of the aqueous chamber; *SV*, canal of Schlemm; *ir*, iris; *io*, divided fibres of the sphincter muscle; *u*, pigment layer or uvea; *ln*, centre of the crystalline lens; *lc*, capsule of the lens; *lce*, epithelium of the lens; *cir*, radiating ciliary muscle; *cio*, divided annular fibres; *cip*, ciliary process; *Ch*, choroid; *R*, retina; *o*, ora serrata; *rc*, the ciliary part of the retina; *h*, hyaloid membrane; *Z*, zonule of Zinn; *P*, some of its fibres spreading out to become attached to the capsule of the lens; *am*, anterior margin of the vitreous humour, *V*.

the vitreous humour ; but after death they may be distended with air : if this be done after removal of the anterior parts which support and enclose it, the folds of the suspensory ligament, which correspond with the eminences and depressions of the ciliary processes, are distended, and the appearance of a sacculated canal (*canal of Petit*), encircling the lens, is produced as in fig. 361.

According to the account usually given, the hyaloid membrane divides in front into two layers ; an anterior, continued forwards as the zonule of Zinn, and a posterior, passing behind the lens ; the canal of Petit being contained between them. The above description is based upon a renewed original investigation into the relations of the structures which support the lens, and is confirmatory of the statements of Merkel, Henle, Brailey, and others, and opposed to those of Iwanoff.

Fig. 361.

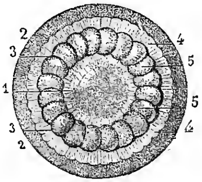


Fig. 361.—View from before of the canal of Petit inflated (from Sappey).

The anterior parts of the sclerotic, choroid, iris and cornea having been removed, the remaining parts are viewed from before, and the canal of Petit has been inflated with air through an artificial opening. 1, front of the lens; 2, vitreous body ; 3, outer border of the canal of Petit ; 4, outer part of the zonule of Zinn ; 5, appearance of sacculated dilatations of the canal of Petit.

THE LENS.

The lens (*lens crystallina*) is a transparent solid body, of a doubly convex shape, with the circumference rounded off. It is completely enclosed by a transparent elastic membrane known as the *capsule of the lens.* The anterior surface is in contact with the iris towards the pupil, receding from it slightly at the circumference ; the posterior is embedded in the vitreous humour. Around the circumference is the zonula. Its convexity is not alike on the two surfaces, being greater behind ; moreover, the curvature is less at the centre than towards the margin. When in its natural position it measures about $\frac{1}{3}$rd of an inch across, and $\frac{1}{5}$th from before backwards. In a fresh lens, divested of its capsule, the outer portion is soft and easily detached ; the succeeding layers are of a firmer consistence ; and in the centre the substance becomes much harder, constituting the so-called "nucleus." On the anterior and posterior surfaces are faint white lines directed from the poles towards the circumference ; these in the adult are somewhat variable and numerous on the surfaces (fig. 363), but in the fœtal lens throughout, and towards the centre of the lens in the adult, they are three in number, diverging from each other like rays at equal angles of 120° (fig. 364). The

Fig. 362.

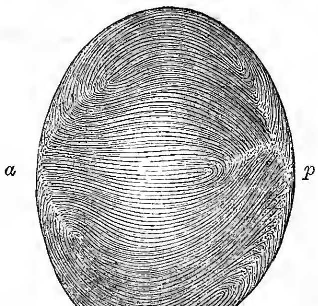


Fig. 362.—The lens viewed from its lateral aspect (after Arnold.) $\frac{5}{1}$

a, anterior; *p*, posterior pole. The direction of the superficial fibres is indicated by the curved lines.

lines at opposite poles have an alternating position (not being over one another), thus of those seen on the posterior surface of the fœtal

Fig. 363.

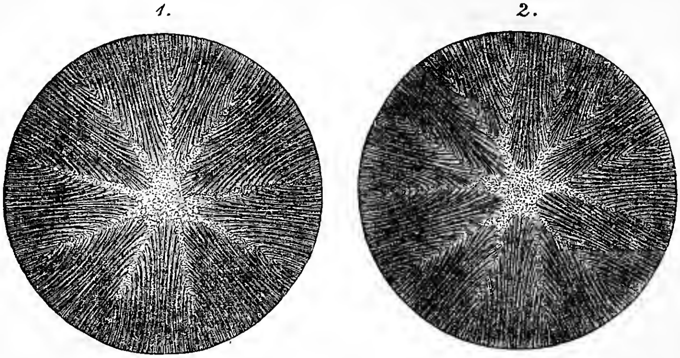


Fig. 363.—1, FRONT VIEW ; 2, HIND VIEW OF THE FIBROUS STRUCTURE OF THE ADULT LENS (after Arnold). $\frac{5}{1}$

lens, one is directed vertically upwards, and the other two downwards and to either side, whereas those on the anterior surface are

Fig. 364.

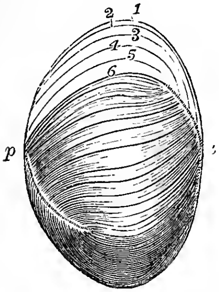


Fig. 364.—DIAGRAM TO ILLUSTRATE THE COURSE OF THE FIBRES IN THE FŒTAL CRYSTALLINE LENS (Allen Thomson).

a, anterior ; *p*, posterior pole.

directed one directly downwards and the other two upwards and to the sides. These lines are the edges of planes or septa within the lens diverging from the axis, and receiving the ends of the lens-fibres, which here abut against one another. As Tweedy has pointed out, they may be seen, by the aid of the ophthalmoscope, even during life. The rays seldom meet at a point, but usually along a somewhat irregular line or area.

Structure.—When the lens has been hardened and the capsule removed, a succession of concentric laminæ may be detached from it like the coats from an onion. They are not continuous, but separate into parts opposite the radiating lines above described (fig. 365). The laminæ are composed of long, riband-shaped, microscopic fibres, $\frac{1}{5000}$ inch broad, which adhere together by their edges, the latter being often finely serrated (fig. 366, A), and pass in a curved direction from the intersecting planes of the anterior half of the lens to those of the posterior half, or *vice versâ:* in this course no fibre passes from one pole to the other, but those fibres which begin near the pole or centre of one surface, terminate near the marginal part of a plane on the opposite surface, and conversely ; the intervening fibres passing to their corresponding places between. The arrangement will be better understood by a reference to fig. 364, where the course of the fibres in the fœtal lens is diagrammatically indicated.

The lens-fibres, as the history of their development shows, are to be looked upon as much elongated cells. In the young state each has a clear oval nucleus, but in the fully-formed lens the nuclei have dis-

Fig. 365.

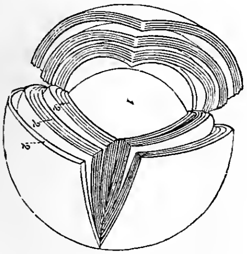


Fig. 365.—LAMINATED STRUCTURE OF THE CRYSTALLINE LENS, SHOWN AFTER HARDENING IN ALCOHOL (Arnold). $\frac{4}{1}$

1, nucleus; 2, 2, lamellæ.

Fig. 366.

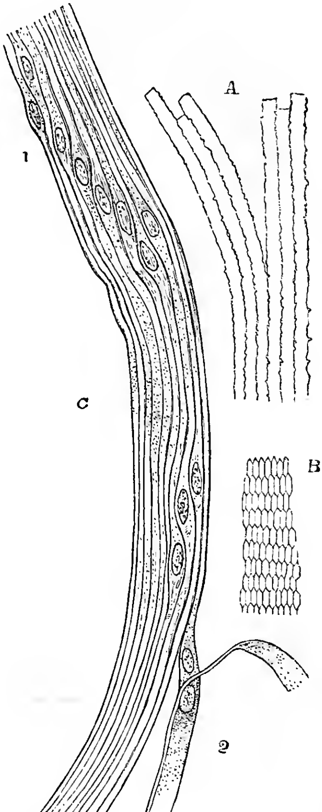


Fig. 366.—FIBRES OF THE CRYSTALLINE LENS. 350 DIAMETERS.

A, longitudinal view of the fibres of the lens from the ox, showing the serrated edges. B, transverse section of the fibres of the lens from the human eye (from Kölliker). C, longitudinal view of a few of the fibres from the equatorial region of the human lens (from Henle). Most of the fibres in C are seen edgeways, and, towards 1, present the swellings and nuclei of the "nuclear zone;" at 2, the flattened sides of two fibres are seen.

appeared from the fibres which form the more internal parts of the lens, and only remain in the most superficial layers. Here they are found, not quite in the middle of each fibre, but slightly nearer the anterior end, their situation nearly corresponding in adjacent fibres, and they form by their juxtaposition the so-called "nuclear zone" around the lens. The superficial fibres further differ from the more deeply seated ones in being softer, and in possessing a plain, unserrated margin. The extremities of all the fibres are softer and more readily acted on by reagents than the middle parts, and the axial or more internal part of a fibre more so than the external, but the transition is gradual from one to the other, and there is no definite membrane enclosing each fibre. The lens-fibres when cut across are seen to be six-sided prisms (fig. 366 B). By reason of this shape, and the serrations of their edges, they fit very exactly the one to the other with but little interfibrillar cementing substance between. This is met with in rather larger quantity in the intersecting planes between the ends of the fibres.

Thin and Ewart have shown that with certain methods of treatment the

superficial lens-fibres show indications of being composed of a number of regular segments separated by sharply marked lines of inter-segmental substance.

Epithelium of the capsule.—At the back of the lens the fibres are directly in contact with the inner surface of the capsule, but in front they are separated from the latter by a single layer of flattened, polygonal, nucleated cells, which covers the whole anterior surface underneath the capsule. Towards the edge or equator of the lens the appearance and character of these cells undergo a change : they first gradually take on a columnar form, and then, becoming more and more elongated, present every transition to the nucleated lens-fibres of the superficial layers, into which they are directly continuous. This transition is more easily traced in the lens of some animals than in man (see fig. 367).

Fig. 367.

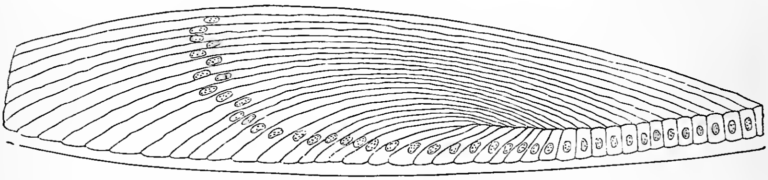


Fig. 367.—Section through the margin of the rabbit's lens, showing the transition of the epithelium into the lens-fibres (Babuchin).

The **capsule** of the lens is a transparent, structureless membrane, somewhat brittle and elastic in character, and when ruptured the edges roll outwards. The fore part of the capsule, from about $\frac{1}{16}$ inch from the circumference, where the anterior part of the suspensory ligament joins it, is much thicker than the back : at the posterior pole of the lens the capsule is very thin indeed. In the adult it, like the lens itself, is entirely non-vascular, but in the fœtus there is a network of vessels in the capsule, supplied by the terminal branch of the central artery of the retina, which passes from the optic papilla through the canal of Stilling in the vitreous humour to reach the back of the capsule, where it divides into radiating branches. After forming a fine network, these turn round the margin of the lens and extend forwards to become continuous with the vessels in the pupillary membrane and iris.

After death a small quantity of fluid (liquor Morgagni) frequently collects between the back of the lens and the capsule : it appears to be derived from the lens-fibres. There is no epithelium in this situation as in front.

Changes in the lens with age.—In the *fœtus*, the lens is nearly spherical (fig. 368, *a*) : it has a slightly reddish colour, is not perfectly transparent, and is softer, and more readily broken down than at a more advanced age.

Fig. 368.

Fig. 368.—Side view of the lens at different ages.

a, at birth with the deepest convexity ; *b*, in adult life with medium convexity ; *c*, in old age with considerable flattening of the curvatures.

In the *adult*, the anterior surface of the lens is distinctly less convex than the posterior (fig. 368, *b*) ; and the substance of the lens is firmer, colourless, and transparent.

In *old age*, it is more flattened on both surfaces (*c*) ; it assumes a yellowish or amber tinge, and is apt to lose its transparency as it gradually increases in toughness and specific gravity.

AQUEOUS HUMOUR AND ITS CHAMBER.

The aqueous humour fills the space in the fore part of the eyeball, between the capsule of the lens with its suspensory ligament and the cornea. The iris, resting in part upon the lens, divides the aqueous chamber partially into two, named respectively the anterior and posterior chambers. This subdivision is incomplete in the adult, but in the fœtus before the seventh month it is completed by the membrana pupillaris, which, by its union with the margin of the pupil, closes the aperture of communication between the two chambers.

The *anterior chamber* is limited in front by the cornea and behind by the iris, while opposite the pupil it is bounded by the front of the lens and its capsule.

The *posterior chamber* was originally so named in the belief that a distinct free space intervened between the iris and the capsule of the lens. It is now, however, well ascertained by observations on the living eye, and by sections made in the frozen state, that the iris comes into contact with the capsule of the lens, both at the pupillary margin and at the adjoining part of the posterior surface; and the term posterior chamber can therefore only be applied to the angular interval existing at the circumference between the ciliary processes, the iris, and the zonula (fig. 360, *ap.*)

Recent Literature of the Eye.—On the macroscopic anatomy of the eye:—*F. Merkel*, Article in Graefe & Saemisch' Handbuch d. gesammt. Augenheilkunde, I. Bd., 1 Th., 1874; *Heinlein*, in Arch. f. Ophthalm., XXI., 1875 (lachrymal canals); *Löwe*, in Arch. f. mikr. Anat., XV., 1878; *J. Gerlach*, Beiträge, &c., Leipzig, 1880; *Angelucci*, in Arch. f. mikr. Anat., XIX., 1880 (structure and devel. of anterior part of bulb).

On the eyelid and conjunctiva:—*Waldeyer*, in Graefe & Saemisch' Handb., 1874; *Longworth*, in Arch. f. mikr. Anat., XI. (nerves); *Ciaccio*, in Mem. d. accad. di Bologna, IV., 1874, and in Moleschott's Unters., XI., 1874; *Reich*, in Arch. f. Ophthalm., XXII., 1875; *Robin et Cadiat*, in J. d. l'anat., 1875 (lachrymal ducts); *Waltzberg*, "Bau der Thränenwege," &c., Rostock, 1876; *Sattler*, in Arch. f. mikr. Anat., 1877; *Tartuferi*, in Giorn. internaz. d. sci. med., 1879 (epithelium of eyelid), and in Archiv. d. sci. med., IV., 1879 (glands of eyelid); *Baumgarten*, in Arch. f. Ophth., XXVI., 1880.

On the cornea and sclerotic:—*Waldeyer*, in Graefe & Saemisch' Handbuch, 1874; *Thanhoffer*, in Virchow's Arch., LXIII., 1875; *Ciaccio*, in Mem. d. accad. di Bologna, V., 1875; *Meyerowitz*, "Mikr. Untersuch." &c., Leipzig, 1875; *Eberth*, in Zürich Untersuch. 3, 1875; *Swaen*, in Bull. de l'acad. de Belgique, 1876; *Raelmann*, in Arch. f. Ophth., XXIII., 1877; *Leber*, in Arch. f. Ophth., 1878 (intercellular spaces in epith.); *Stirling and Skinner*, in the J. of Physiol., I., 1878; *Heisrath*, in Arch. f. Ophth., XXVI. (communication of anterior chamber with canal of Schlemm).

On the choroid coat and iris:—*Iwanoff*, in Graefe and Saemisch' Handb., 1874; *Michel*, Structur d. Iris-stroma, Erlangen, 1875; *Faber*, Bau d. Iris, Leipzig, 1876; *Sattler*, in Arch. f. Ophthalm., XXII., 1876; *J. Gerlach*, in Erlangen Sitzungsb., 1879; *Meyer*, in Arch. f. mikr. Anat., XXII., 1879 (nerves of iris).

On the retina:—*M. Schultze*, Article in Stricker's Handbook, 1871; *Schwalbe*, in Graefe and Saemisch' Handb., 1874; *Michel*, in Beiträge, &c., als Festgabe an C. Ludwig, 1875 (arrangement of fibres in nerve-fibre layer); *W. Müller*, in the same work (morphological); *Merkel*, in Arch. f. Ophthalm., XXII., 1876; *W. Krause*, Die Nervenendigung in der Retina, in Arch. f. mikr. Anat., XII., 1876; *Boll*, in Monatsbericht d. Berlin Akad., 1876, 1877; and in Arch. f. (Anat. u.) Phys., 1877; *Kühne*, in Med. Centralbl., 1877 & 1878; and in Heidelb. Unters., I., 1877, and II., 1878; and with *Ewald* in the same; *Kuhnt*, in Monatsbl. f. Augenheilk., 1877, and in Med. Centralb., 1877 (pigment epithelium); *Gunn*, in J. of Anat. and Phys., 1877; *Angelucci*, in Arch. f. (Anat. u.) Phys., 1878 (retinal pigment); *Dennisenko*, in Arch. f. mikr. Anat., 1880; *Retzius*, Biol. Unters., Stockholm, 1881.

On the lens and vitreous humour:—*Arnold*, in Graefe and Saemisch' Handb.; and *Schwalbe* (vitreous) in the same, 1874; *Hosch*, in Arch. f. Ophthalm., XX., 1874; *Thin and Ewart*, in the Journ. of Anat., 1876; *Ritter*, in Arch. f. Ophth., XXIII., 1877;

Henle, Göttinger Abhandl., XXIII., 1879 ; *Brailey*, in Guy's Hosp. Reports, XXIV., 1879 (suspensory apparatus of lens) ; *Ulrich* (canal of Petit), in Arch. f. Ophthalm., XXVI.

On the blood-vessels and lymphatics of the eye.—*Leber*, in Graefe and Saemisch' Handb., 1874. Of the eyelids : *Fuchs*, in Arch. f. Ophth., 1878, and in Med. Centralbl., 1878 ; and *Langer*, in Med. Jährb., 1878. Of the retina : *Nettleship*, in Ophth. Hosp. Reports, 1875 ; *Hesse ; His*, in Arch. f. Anat. (u. Phys.), 1880 ; *O. Becker*, in Arch. f. Ophth., 1881.*

THE EAR.

The organ of hearing is divisible into three parts : the external ear (fig. 369, 1, 2), the tympanum or middle ear (3), and the labyrinth or internal ear (6). The first two of these are to be considered as accessories to the third, which is the sentient portion of the organ.

Fig. 369.

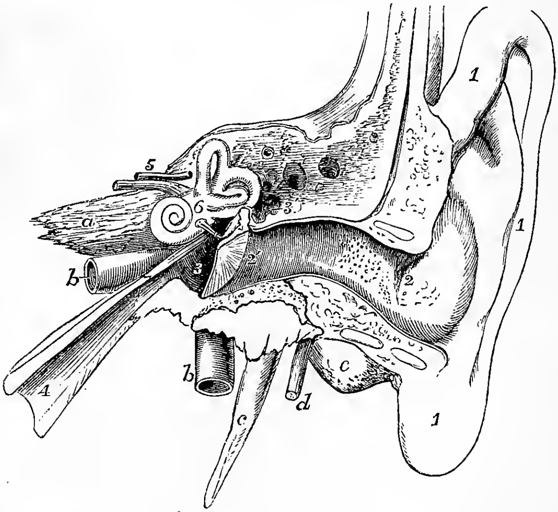


Fig. 369.—Diagrammatic view from before of the parts composing the organ of hearing of the left side (after Arnold).

The temporal bone of the left side, with the accompanying soft parts, has been detached from the head, and a section has been carried obliquely through it so as to remove the front of the meatus externus, half the tympanic membrane, and the upper and anterior wall of the tympanum and Eustachian tube. The meatus internus has also been opened, and the bony labyrinth exposed by the removal of the surrounding parts of the petrous bone. 1, the pinna and lobe ; 2 to 2′, meatus externus ; 2′, membrana tympani ; 3, cavity of the tympanum ; above 3, the chain of small bones ; 3′, opening into the mastoid cells ; 4, Eustachian tube ; 5, meatus internus, containing the facial (uppermost) and auditory nerves ; 6, placed on the vestibule of the labyrinth above the fenestra ovalis ; *a*, apex of the petrous bone ; *b*, internal carotid artery ; *c*, styloid process ; *d*, facial nerve issuing from the stylo-mastoid foramen ; *e*, mastoid process ; *f*, squamous part of the bone.

THE EXTERNAL EAR.

In the external ear are included the *pinna*—the part of the outer ear which projects from the side of the head—and the *meatus* or passage which leads thence to the tympanum, and which is closed at its inner extremity by a membrane interposed between it and the middle ear.

* The elder literature of the eye will be found in the several articles referred to in the Handbuch der gesammten Augenheilkunde, 1874.

THE PINNA.

The general form of the pinna or auricle, as seen from the outside, is concave, to fit it for collecting and concentrating the undulations of sound, but it is thrown into various elevations and hollows, to which distinct names have been given. The largest and deepest concavity is called the *concha* (fig. 370, 7); it surrounds the entrance to the meatus, and is interrupted at its upper and anterior part by a ridge, which is the beginning of the helix. In front of the concha, and projecting backwards over the meatus, is a conical prominence, the *tragus* (fig. 370, 6), covered usually with hairs. Behind this, and separated from it by a deep notch, is another smaller elevation, the *antitragus* (5). Beneath the antitragus, and forming the lower end of the auricle, is the *lobule* (8), which is devoid of the firmness and elasticity that characterise the rest of the pinna. The thinner and larger portion of the pinna is bounded by a prominent and incurved margin, the *helix* (1), which, springing above and rather within the tragus, from the hollow of the concha, surrounds the upper and posterior margin of the auricle, and gradually loses itself in the back part of the lobule. Within the helix is another curved ridge, the *antihelix* (3), which, beginning below at the antitragus, sweeps round the hollow of the concha, forming the posterior boundary of that concavity, diverging above it into two ridges. Between the helix and the antihelix is a narrow curved groove, the *fossa of the helix* (fossa scaphoidea) (2); and in the fork of the antihelix is a somewhat triangular depression, the *fossa of the antihelix* (fossa triangularis) (4).

Fig. 370.

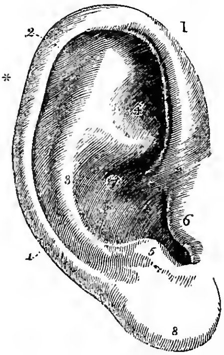


Fig. 370.—Outer surface of the pinna of the right auricle. $\frac{2}{3}$

1, helix; 2, fossa of the helix; 3, antihelix; 4, fossa of the antihelix; 5, antitragus; 6, tragus; 7, concha; 8, lobule.

A slight pointed projection which is occasionally observed in the human subject at the margin of the helix (at a place indicated by the asterisk in fig. 370) is of interest as representing the much more distinct pointed extremity met with in the expanded ears of quadrupeds (Darwin, "The Descent of Man," 2nd edition, p. 15). The point in question is distinctly seen in the cartilage represented in fig. 371.

Structure.—The pinna consists mainly of yellow fibro-cartilage and integument, with a certain amount of adipose tissue. It has several ligaments and small muscles of minor importance.

The *skin* covering it is thin, closely adherent to the cartilage, and contains sebaceous follicles, which are most abundant in the hollows of the concha and scaphoid fossa.

The *cartilage* (fig. 371, A, B) forms a thin plate, presenting all the inequalities already described as apparent on the outer surface of the pinna, and on its cranial surface having prominences the reverse of the concha and the fossa of the helix, while between these is a depression in

the situation of the antihelix. The cartilage is not confined to the pinna, but enters likewise into the construction of the outer part of the external auditory canal. When dissected from other structures, it is seen to be attached by fibrous tissue to the rough and prominent margin of the external auditory meatus of the temporal bone. The tubular part is cleft in front between the tragus and fore part of the helix inwards to the bone, the deficiency being filled with fibrous membrane ; the whole cartilage may be looked upon as an elongated plate, the lower part of which is folded round in front so as to bring it nearly into contact with the upper part. There is no cartilage in the lobule : it contains only fat and tough connective tissue.

Behind the prominence of cartilage which forms the antitragus is a deep notch, separating it from the cartilage of the helix, which here forms a tail-like process descending towards the lobule. At the fore part of the pinna, opposite the first bend of the helix, is a small conical projection of the cartilage, called the *process of the helix*, to which the anterior ligament is attached. Behind this process is a short vertical slit in the helix ; and on the surface of the tragus is a similar but somewhat longer fissure. A deep fissure passes back between the commencement of the helix and the tube of the ear, and another passing outwards and backwards from the deep end of the longitudinal cleft separates the part forming the tragus from the rest of the tube, so that the tube is continuous with the pinna only by means of a narrow isthmus. One or two other irregular gaps or fissures partially divide the cartilaginous tube transversely, and the whole of these deficiencies are termed *fissures of Santorini*. The substance of the cartilage is very pliable, and is covered by a firm fibrous perichondrium.

Of the *ligaments of the pinna*, the most important are two, which assist in attaching it to the side of the head. The *anterior* ligament, broad and strong, extends from the process of the helix to the root of the zygoma. The *posterior* ligament fixes the back of the auricle (opposite the concha) to the outer surface of the mastoid process of the temporal bone. A few fibres attach the tragus also to the root of the zygoma. Ligamentous fibres are likewise placed across the fissures and intervals left in the cartilage.

Of the *muscles of the pinna*, those which are attached by one end to the side of the head, and move the pinna as a whole, have been already described (vol. i.) : there remain to be examined several smaller muscles, composed of thin layers of pale-looking fibres, which extend from one part of the pinna to another, and may be named the special muscles of the organ. Six such small muscles are distinguished ; four being placed on the outer and two on the inner or deep surface of the pinna.

The *smaller muscle of the helix* (fig. 371, 1) is a small bundle of oblique fibres, lying over, and firmly attached to, that portion of the helix which springs from the bottom of the concha.

The *greater muscle of the helix* (2) lies vertically along the anterior margin of the pinna. By its lower end it is attached to the process of the helix ; and above, its fibres terminate opposite the point at which the ridge of the helix turns backwards.

The *muscle of the tragus* (3) is a flat bundle of short fibres covering the outer surface of the tragus : its direction is nearly vertical. Occasionally a slender bundle of muscular fibres is seen prolonging this muscle across the cleft in the cartilage between the tragus and fore part of the helix.

The *muscle of the antitragus* (4) is placed obliquely over the antitragus and behind the lower part of the antihelix. It is fixed at one end to the antitragus, from which point its fibres ascend to be inserted into the tail-like extremity of the helix, above and behind the lobule.

The *transverse muscle* (5) lies on the inner or cranial surface of the pinna, and consists of radiating fibres which extend from the back of the concha to the prominence which corresponds with the groove of the helix.

The *oblique muscle* (Tod) (6) consists of a few fibres stretching from the back

of the concha to the convexity directly above it, across the back of the inferior branch of the antihelix, and near the fibres of the transverse muscle.

Vessels and nerves of the pinna.—The auricular branch of the *posterior auricular artery*, a branch from the external carotid, is distributed chiefly on the inner surface, but sends small branches round and through the cartilage to ramify on the outer surface of the pinna. Besides this artery, the auricle receives the *anterior auricular* from the superficial temporal.

Fig. 371.

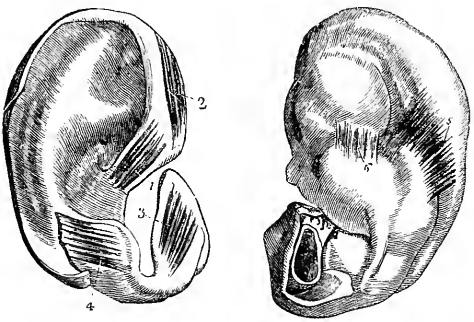


Fig. 371, A and B.—Outer and inner surfaces of the right pinna, exposed to show the small muscles (from Arnold).

1, musculus helicis minor; 2, m. helicis major; 3, tragicus; 4, antitragicus; 5, musculus transversus auriculæ; 6, musculus obliquus auriculæ.

The *veins* for the most part accompany the arteries. They join the posterior auricular and temporal veins. The *great auricular nerve*, from the cervical plexus, supplies the greater part of the inner surface of the auricle, and sends small filaments with the posterior auricular artery to the outer surface of the lobule and the part of the ear above it. The auricular branch of the *posterior auricular nerve*, derived from the facial, after communicating with the *auricular branch of the pneumogastric*, ramifies on the back of the ear and supplies the retrahent muscle. The anterior and upper muscles of the auricle receive their supply from the *temporal branches* of the facial nerve. The *auriculo-temporal* branch of the third division of the fifth nerve gives filaments chiefly to the outer surface of the pinna. A branch of the *small occipital* supplies the upper part of the inner surface.

THE EXTERNAL AUDITORY CANAL.

The external auditory canal, *meatus auditorius externus* (369, 2, 2), extends from the bottom of the concha to the membrane of the tympanum and serves to convey the vibrations of sound to the middle chamber of the ear. The canal is about $1\frac{1}{4}$ inches long. In its inward course it is inclined somewhat forwards (fig. 372); and it has likewise a distinct vertical curve (fig. 369), being at first directed somewhat upwards, and afterwards turning over a convexity in the floor of the osseous part to dip downwards to its termination. The calibre of the passage is smallest about the middle. The outer opening is largest from above downwards, but the inner end of the tube is slightly wider in the transverse direction. At the inner extremity the tube is terminated by the membrana tympani, which is placed obliquely, being inclined downwards, forwards, and towards the mesial plane; and thus, as shown in fig. 369, the floor of the meatus is longer than its roof.

The meatus is composed partly of cartilage, and partly of bone, and is lined by a prolongation of the skin.

The *cartilaginous* part occupies somewhat less than half the length of the passage. It is formed, as already mentioned, by an inflection of the deep part of the cartilage of the pinna.

The *osseous portion* is a little longer and rather narrower than the car-

tilaginous part. At its inner end is a narrow groove, which extends round the sides and floor of the meatus, but is deficient above; into this the margin of the membrana tympani is inserted.

The skin of the meatus is continuous with that covering the pinna, but is very thin, especially in the osseous part, and becomes gradually thinner towards the bottom of the passage. In the osseous part it

Fig. 372.

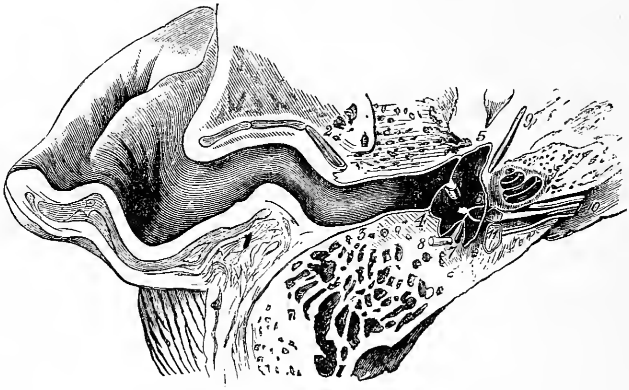


Fig. 372.—View of the lower half of the auricle and meatus in the left ear divided by a nearly horizontal section (after Rüdinger).

1. Posterior wall; 2, anterior wall of the cartilaginous meatus; 3, posterior wall of the bony meatus; 4 to 5, membrane of the tympanum, with the handle of the malleus cut; 6, stapes, to the right of 6, section of the cochlea; 7, stapedius muscle; 8, section of facial nerve; 10, branches of the auditory nerve to the cochlea, saccule, and utricle, 11.

adheres very closely to the periosteum, and at the bottom of the tube is stretched over the surface of the membrana tympani, forming the outer layer of that structure. Towards the outer part the skin possesses fine hairs and sebaceous glands; and in the thick subdermic tissue over the cartilage are many small oval glands of a brownish yellow colour, agreeing in form and structure with the sweat glands, but larger (fig. 237 on p. 254). The cerumen or ear-wax is secreted by these glands (*glandulæ ceruminosæ*), and their numerous openings may be seen to perforate the skin of the meatus. Hairs and glands are absent from the bony part of the tube.

Vessels and nerves.—The external auditory meatus is supplied with arteries from the *posterior auricular*, *internal maxillary*, and *temporal* arteries; and with nerves chiefly from the auriculo-temporal branch of the fifth nerve. The principal branches of the arteries course along the upper and back wall of the canal.

State in the infant.—The auditory passage is very short and rudimentary in the infant, for the osseous part begins to grow out of the temporal bone only after birth, and thus the internal and middle parts of the ear are much closer to the surface than in the adult (vol. i. p. 71).

THE MIDDLE EAR OR TYMPANUM.

The tympanum or drum, the middle chamber of the ear, is a narrow irregular cavity in the substance of the temporal bone, placed between the membrane occluding the inner end of the external auditory canal

and the outer bony wall of the labyrinth. Its width between these boundaries varies from about $\frac{1}{12}$th to $\frac{1}{6}$th of an inch. It contains a chain of small bones, by means of which the vibrations communicated from without to the membrana tympani are conveyed across the cavity to the internal ear, and also certain minute muscles and ligaments, which belong to the bones referred to, as well as nerves, some of which end within the cavity, whilst others merely pass through it to other parts. The cavity is otherwise filled with air, for it communicates with the atmosphere through the Eustachian tube, which leads into the pharynx. A roof and floor, an outer and inner wall, and an anterior and posterior boundary are commonly described.

The *roof* of the tympanum is formed by a thin plate of bone, which may be easily broken through so as to obtain a view of the tympanic cavity from above; it is situated on the upper anterior surface of the petrous portion of the temporal bone, near the angle of union with the squamous portion. The *floor* is narrow, in consequence of the outer and inner boundaries being inclined towards each other. It is separated by a thin plate of bone from the jugular fossa behind and the carotid canal in front.

The *outer wall* is formed, to a small extent, by bone, but mainly by the membrane (*membrana tympani*) already mentioned as closing the inner end of the external auditory meatus. Immediately in front of the ring of bone into which the membrana tympani is inserted, is the inner extremity of the fissure of Glaser. Close to the back of this fissure is the opening of a small canal, through which the chorda tympani nerve passes out from the tympanum.

The **membrana tympani** is an ellipsoidal disc, the longer axis of which is directed from behind and above, forwards and downwards, and

Fig. 373.

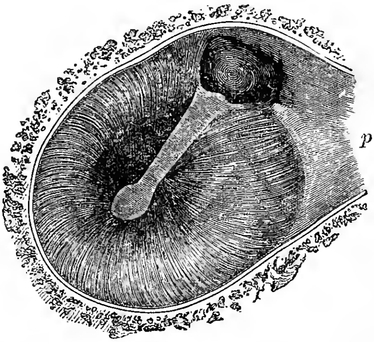


Fig. 373.—View of the outer surface of the left membrana tympani, after removal of the cutaneous layer (E.A.S.). $\frac{4}{1}$

The handle of the malleus is distinctly seen, and the long process of the incus appears as a faint light band parallel with and a little behind the handle of the malleus. The other light band nearly at right angles to the malleus is caused by the chorda tympani nerve. The notch of Rivini is seen above the handle of the malleus. *p*, termination of the posterior wall of the external auditory meatus.

is about 0.37 inches (9.25 mm.) in length: the shorter axis being about 0.33 inches (8.25 mm.). It is inserted into the groove already noticed at the end of the meatus externus, and so obliquely that the membrane inclines towards the anterior and lower part of the canal at an angle of about 55°. The handle of the malleus (fig. 373), one of the small bones of the tympanum, descends in contact with the inner surface of the membrane, covered by mucous membrane, to a little below the centre, where it is firmly fixed; and, as this process of the bone is directed inwards, the outer surface of the membrane is thereby depressed in a conical form.

The membrana tympani is about $\frac{1}{250}$ inch (0.1 mm.) thick. Covering it

externally is a prolongation of the skin of the external meatus; internally is a prolongation of the mucous membrane lining the cavity of the tympanum; and between these two is the proper substance of the membrane, composed of fibrous tissue. The greater number of the fibres radiate from the attachment of the handle of the malleus (fig. 373), but there are also circular fibres which are situated within or mesially to the radial, and closer to the circumference, form a dense, almost ligamentous ring. The radial fibres are not straight, but are slightly bowed outwards, so that between the most depressed point or *umbo*, and the attached border, the membrane is slightly convex outwardly. This shape is maintained by the annular fibres.

At the upper and anterior part, the annular fibres stretch across the mouth of a small notch in the bony ring to which the membrane is attached (notch of Rivini). The notch is occupied by a lax part of the membrane (*membrana flaccida*, Shrapnell), consisting of loose connective tissue, with vessels and nerves, and covered by skin and mucous membrane. It occasionally happens that a fissure or perforation is to be detected at this place.

Fig. 374.

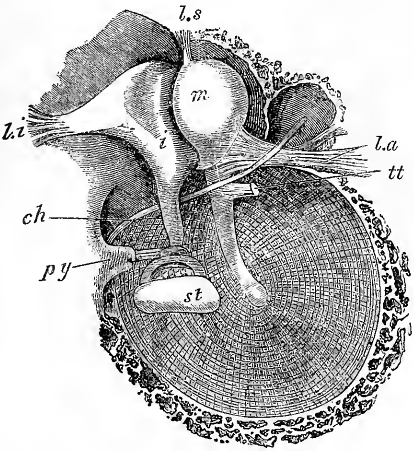


Fig. 374.—View of the left membrana tympani and auditory ossicles from the inner side, and somewhat from above (E.A.S.). $\frac{4}{1}$

m, malleus; *i*, incus; *st*, stapes; *py*, pyramid from which the tendon of the stapedius muscle is seen emerging; *t t*, tendon of the tensor tympani cut short near its insertion; *l a*, anterior ligament of the malleus: the processus gracilis is concealed by the lower fibres of this ligament; *l s*, superior ligament of the malleus; *l. i*, ligament of the incus; *ch*, chorda tympani nerve passing across the outer wall of the tympanum.

The membrane is supplied with blood-vessels, but they are chiefly confined to the skin and mucous membrane covering the surfaces; a few are, however, found in the proper fibrous membrane, and form a communication between the two systems on the surfaces. Those of the skin are mostly supplied by a small artery, derived from the deep auricular branch of the internal maxillary, which passes from above, parallel to and along the handle of the malleus. The nerves for the most part accompany the blood-vessels, first supplying these and then forming a plexus both in the cutis and in the mucosa. Lymphatic vessels are, according to Kessel, tolerably abundant in all three layers.

The **inner wall** of the tympanum, which separates it from the internal ear, is very uneven. Near its upper part is an ovoid, or nearly kidney-shaped opening—*fenestra ovalis* (fig. 375, *f.o*), which leads into the cavity of the vestibule. This opening, which is elongated from before backwards, with a slight inclination downwards in front, is occupied in the recent state by the base of the stapes, and the annular ligament connected with that plate of bone. Above the fenestra ovalis, and between it and the roof of the tympanum, a ridge indicates the position of the aqueduct of Fallopius (*aF*), as it passes backwards, containing the facial nerve.

Below is a larger and more rounded elevation, caused by the projection outwards of the first turn of the cochlea, and named the *promontory*, or *tuber cochleæ* (fig. 375, *p*); its surface is marked by grooves, in which lie the nerves of the tympanic plexus.

Below and behind the promontory, and somewhat hidden by it, is another aperture named *fenestra rotunda,* which lies within a funnel-shaped depression (fig. 375, *f.r*). In the macerated and dried bone the fenestra rotunda opens into the scala tympani of the cochlea; but, in the recent state, it is closed by a thin membrane.

Fig. 375.

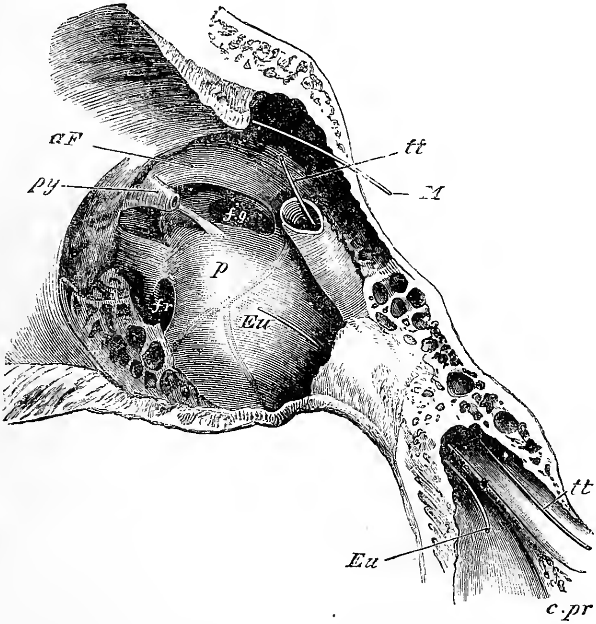


Fig. 375.—Inner wall of the right tympanum (G. D. Thane). $\frac{4}{1}$

The lower end of the Eustachian tube and canal for the tensor tympani is cut open obliquely by the saw. *M*, bristle passed into the opening from the tympanum into the mastoid cells; *f o*, fenestra ovalis; *f r*, fenestra rotunda; *p*, promontory; *a F*, aqueduct of Fallopius, or canal of the facial nerve; *c.pr*, lower end of the processus cochleariformis, cut; *t t*, bristle passed through the canal for the tensor tympani muscle; *Eu*, bristle in the Eustachian tube.

The membrane closing the fenestra rotunda—*secondary membrane of the tympanum* (Scarpa)—is rather concave towards the tympanic cavity, and, like the membrana tympani, is composed of three structures, the middle being fibrous, and the outer and inner derived from the membranes lining the cavities between which it interposed, viz., the tympanum and the cochlea.

The **posterior wall** of the tympanum has at its upper part one larger (fig. 375, *M*), and several smaller openings, which lead into irregular cavities, the *mastoid cells*, in the substance of the mastoid portion of the temporal bone. These cells communicate for the most part freely with one another, and are lined by a thin mucous membrane continuous with

that of the tympanum. Behind the fenestra ovalis, and directed upwards, is a small conical eminence, called the *pyramid*, or *eminentia papillaris* (fig. 374, 375, *py*). Its apex is pierced by a foramen, through which the tendon of the stapedius muscle emerges from a canal which when traced back is found to turn downwards in the posterior wall of the tympanum, and to join obliquely the descending part of the aqueduct of Fallopius (fig. 372, 7). A small bony spiculum often connects the end of the pyramid with the upper part of the promontory (see fig. 375).

The anterior extremity of the tympanum is narrowed by the gradual descent of the roof, and is continued into the inner orifice of the

Fig. 376.

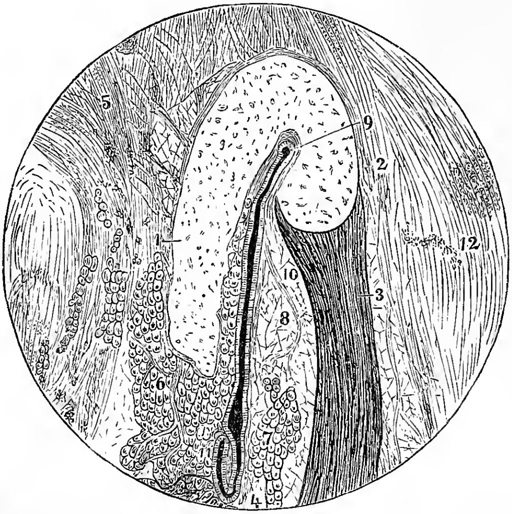


Fig. 376.—Section across the cartilaginous part of the Eustachian tube. (Rüdinger).

1, 2, bent cartilaginous plate ; 3, musc. dilatator tubæ ; to the left of 4, part of the attachment of the levator palati muscle ; 5, tissue uniting the tube to the base of the skull ; 6, and 7, mucous glands ; 8, 10, fat ; 9 to 11, lumen of the tube ; 12, connective tissue on the lateral aspect of the tube.

Eustachian tube (fig. 375). Above the commencement of this is the canal which lodges the tensor tympani muscle. This canal is about half an inch long, and it opens immediately in front of the fenestra ovalis, surrounded by the expanded and everted end of the cochleariform process which separates it from the Eustachian tube.

In the recent state the fibrous sheath of the tendon is expanded over the end of the canal, so as to impart to it a conical shape (see fig. 381, *tt*.)

The **Eustachian tube** (fig. 369, 4) is a canal, bounded partly by bone, partly by cartilage and fibrous membrane, which leads from the cavity of the tympanum to the upper part of the pharynx. From the tympanum it is directed forwards and inwards, with a slight inclination downwards ; its entire length is about an inch and a half. The posterior or *osseous* division of the tube is placed at the angle of junction of the petrous portion of the temporal bone with the squamous portion. The *anterior* part of the tube is formed of a triangular piece of cartilage, the edges of

which are slightly curled round towards each other, leaving an interval at the under and outer side, in which the wall of the canal is completed by dense but pliable fibrous membrane, and by a muscular band connected with the tensor palati and termed by Rüdinger the *dilatator tubæ*. The tube is trumpet-shaped, being narrow behind, and gradually expanding to a greater width in front; the anterior part is compressed from side to side, and is fixed to the inner pterygoid plate of the sphenoid bone. The anterior opening is of a compressed oval form, and is placed obliquely at the side and upper part of the pharynx, into which its prominent margin projects behind the lower turbinate bone of the nose, and above the level of the hard palate. Through this aperture the mucous membrane of the pharynx is continuous with that which lines the tympanum, and under certain conditions air passes into and out of that cavity.

SMALL BONES OF THE EAR.—Three small bones (*ossicula auditûs*) are contained in the upper part of the tympanum: of these, the outermost (*malleus*) is attached to the membrana tympani; the innermost (*stapes*) is fixed in the fenestra ovalis; and the third (*incus*) placed between the other two, is connected to them by articular surfaces. They form together an angular and jointed connecting rod between the membrana tympani and the membrane which closes the fenestra ovalis.

The **malleus** or hammer-bone (figs. 377, 378), consists of an upper

Fig. 377.—THE LEFT MALLEUS OF THE ADULT VIEWED FROM THE OUTER SIDE. MAGNIFIED FOUR TIMES. (After Helmholtz.)

c, capitulum; *a i*, grooved articular surface for the incus; *e*, its prominent lower margin; *d*, cervix; *m*, end of the manubrium; *b*, processus brevis; *pr.gr*, processus gracilis, here represented only by a short stump, the rest of the process having been converted into ligament; *a*, ridge to which the external ligament is attached.

Fig. 377.

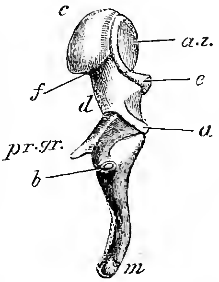


Fig. 378.

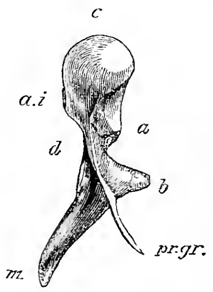


Fig. 378.—LEFT MALLEUS OF A CHILD VIEWED FROM BEFORE. MAGNIFIED FOUR TIMES. (E.A.S.)

The lettering is the same as in the previous figure. The processus gracilis is here complete. The angle which the manubrium forms with the rest of the bone is seen in this view.

thicker portion, with a tapering lower portion, and two processes. The upper end is formed by the rounded *head* (capitulum) (*c*), on the posterior surface of which is an elliptical depressed surface (*a.i*) with prominent margins, which passes obliquely downwards and inwards, and serves for articulation with the incus. Below the head is a constricted *neck* (*d*); and beneath this another slight enlargement of the bone, to which the processes are attached. The *handle* (*manubrium*) (*m*), the lower tapering point of the malleus, is slightly twisted, and is compressed from before backwards to near its point, where it is flattened laterally. It forms a rounded obtuse angle with the head of the bone (fig. 378), and passes downwards, with an inclination forwards and inwards, on the inner side of the membrana tympani, to which it is closely attached both by its periosteal covering and also by a dense fibro-cartilaginous

tissue extending its whole length, except near the root of the process, where the bone is less firmly united to the membrane. The point of insertion of the tendon of the tensor tympani muscle is sometimes marked by a slight projection on the inner side of the manubrium near its upper end. The *long process* (*processus gracilis* seu *folianus*) (*pr.gr.*) is a very slender spiculum of bone, which in the adult is usually converted, except a small stump, into ligamentous tissue, and even where it still exists as bone is often broken off in its removal from the tympanum; it projects at nearly a right angle from the front of the neck of the malleus, and extends thence obliquely downwards and forwards to the Glaserian fissure. Its end is flattened and expanded, and is connected by ligamentous fibres or bone to the sides of the fissure. The *short process* (*processus brevis* vel *obtusus*) (*b*) is a low conical eminence situated at the root of the manubrium, beneath the cervix, and projecting outwards towards the upper part of the membrana tympani, to which it is attached.

The **incus** (fig. 379), as its name implies, has been compared to an

Fig. 379.

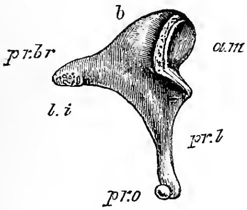


Fig. 379.—Left incus, viewed from the inner side and somewhat from before. Magnified four times (G. D. Thane).

b, body; *a m*, ridged articular surface for the malleus; *pr. br*, processus brevis; *l. i*, rough surface near its extremity for the attachment of the ligament of the incus; *pr. l*, processus longus, terminating below in a small projection which comes off from it at a right angle, and is capped by a convex tubercle, processus orbicularis, *pr. o*, for articulation with the stapes.

anvil; but it resembles perhaps more nearly a tooth with two fangs widely separated. It consists of a body and two processes. The *body* has a deep saddle-shaped articular surface in front (*a. m*), which fits against the head of the malleus. The *shorter process* (*crus breve*) (*pr.br.*) of the incus projects backwards. Its extremity is tipped with cartilage, and is moveably articulated by ligamentous fibres with the posterior and partly with the outer wall of the tympanum near the entrance to the mastoid cells. The *long process* (*crus longum*) (*pr.l*) tapers rather more gradually, and passes downwards and inwards behind and parallel to the handle of the malleus: at its extremity it is bent inwards, and is suddenly narrowed into a short neck; and upon this is set a flattened tubercle (*processus orbicularis* seu *lenticularis*) (*pr.o*), tipped with cartilage. This tubercle, which articulates with the head of the stapes, was formerly, under the name of *os orbiculare* seu *lenticulare*, described as a separate bone, which indeed it originally is in childhood.

At the joints between the incus and malleus on the one hand and the incus and stapes on the other the articular surfaces are tipped with cartilage and enclosed by a synovial membrane. Rüdinger describes both in this joint and in the articulation of the incus with the stapes an interarticular fibro-cartilage, which subdivides the joint into two parts.

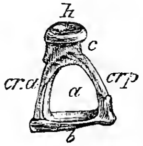
The **stapes** (fig. 380), the third and innermost bone of the ear, is in shape remarkably like a stirrup, and is composed of a head, a base, and two crura. The *head* (*h*) is directed outwards, and has on its end a slight depression, covered with cartilage, which articulates with the lenticular process of the incus. The *base* (*b*) is a plate of bone fitting into

the fenestra ovalis, but not quite closely, so that a slight amount of movement is allowed. Its form is irregularly oval, the upper margin being curved, while the lower is nearly straight (fig. 374, *st*). Its border is encircled by hyaline cartilage, which also covers its vestibular surface. The margin of the fenestra ovalis has also a covering of the same tissue (Toynbee), and the opposed cartilaginous surfaces are closely connected by a network of elastic fibres passing between them, and forming an especially dense

Fig. 380.—Left stapes, viewed from below. Magnified four times. (E.A.S.)

h, outer extremity or head of the bone, with a shallow concavity for articulation with the orbicular process of the incus; *c*, constricted part or cervix. This is not always so well-marked as in the present specimen. *cr a*, anterior crus; *cr p*, posterior crus; *b*, base; *a*, arch of the stapes. The bony groove which bounds the arch is shown in front and below; above and behind it is concealed from view.

Fig. 380.



ligamentous band near the tympanic and vestibular cavities (Rüdinger). The crura of the stapes diverge from a constricted part (*neck*, fig. 380, *c*) of the bone, situated close to the head, and are attached to the outer surface of the base near its extremities. The anterior crus (*cr. a*) is the shorter and straighter of the two. The crura, with the base of the stapes, encircle a small triangular or arched space (*a*), across which in the recent state a thin membrane is stretched. A shallow groove runs round the opposed surfaces of the arch, and into this the membrane is received.

Ligaments.—In the articulations of the small bones of the ear with one another the connection is strengthened by ligamentous fibres.

Their attachment to the walls of the tympanum is effected chiefly by the following ligaments, as well as by the reflections of the mucous membrane lining that cavity.

The *anterior ligament of the malleus* (figs. 374, *l. a*, and 381, *l. a. m*) is a comparatively strong and broad band of fibres, which connects the base of the processus gracilis and the anterior part of the body of the malleus above this process with the anterior wall of the tympanum close to the Glaserian fissure. The part of the ligament which passes out of the Glaserian fissure, was long thought to be muscular (laxator tympani auct.), but most observers agree in denying the existence of muscular tissue in this situation. Many of the fibres of the anterior ligament take origin from a bony prominence which projects from the margin of the external meatus into the tympanum, and forms the anterior boundary of the notch of Rivini. This prominence is known as the larger spinous process of the tympanum (spina tympanica major) (fig. 381, *sp*) to distinguish it from another bony prominence or spine at the posterior extremity of the notch.

Accessory anterior ligament.—A comparatively stout sheath surrounds the tendon of the tensor tympani as it passes from the end of the cochleariform process to the malleus, and a flat ligamentous band with a thickened margin (fig. 381, *l*), which lies along the anterior border of this sheath, stretching between the anterior wall of the tympanum and the upper part of the manubrium and neck of the malleus may be regarded as assisting in the fixation of the malleus anteriorly (E.A.S.).

The *external ligament of the malleus* (fig. 381, *l.e.m.*), is a fan-shaped ligamentous structure, the fibres of which arise from the margin of the

notch of Rivini, and converge to the short process and adjacent part of the body of the malleus.

The posterior bundle of fibres of this ligament together with the anterior bundle of the anterior ligament are termed by Helmholtz the "axis-ligament of the malleus," since they are attached nearly in the axis of rotation of that bone.

Fig. 381.

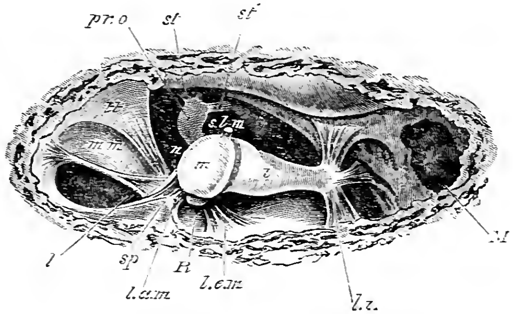


Fig. 381.—View of the cavity of the tympanum, opened from above. (Magnified four times.) (E. A. S.)

m, head of the malleus; *sp*, spina tympanica major; *l. a. m*, anterior ligament of the malleus; *l. e. m*, external ligament of the malleus; *R*, gap between the two ligaments leading to the membrana flaccida and notch of Rivini; *i*, body of the incus; *l. i*, posterior ligament of the incus: *pr. o*, processus orbicularis of the incus seen in the depth of the cavity, articulated with the head of the stapes, *st*; *st'*, tendon of the stapedius muscle emerging from the pyramid; *tt*, tendon of the tensor tympani, emerging from the conical end of its canal; *l*, thickened edge of a flattened band of ligamentous fibres which lies in a fold of the mucous membrane, *m.m.*, and assists in fixing the malleus; *s. l. m*, superior ligament of the malleus, cut short; *n*, chorda tympani nerve.

The *superior ligament of the malleus* (figs. 374, *l.s.*, and 381, 382. *s. l. m*), consists of a small bundle of fibres, which passes downwards and outwards from the roof of the tympanum to the head of the malleus, and serves to check the outward movements of the manubrium and membrana tympani.

Inferior ligament of the malleus.—A small bundle of ligamentous fibres is frequently found passing from near the extremity of the handle of the malleus upwards and backwards behind the long process of the incus, to be attached to the outer wall of the tympanum. This ligament assists the external ligament in resisting a too violent action of the tensor tympani muscle, and it serves also to restrict any rotating action which that muscle may tend to exert upon the malleus (E.A.S.).

The *ligament of the incus* (figs. 374, 381, *l. i*) extends from near the point of the short crus backwards towards the posterior wall of the tympanum, but some of its fibres spread also outwards and inwards. It is attached below the entrance to the mastoid cells.

Muscles.—There are only two well-determined muscles of the tympanum. Sömmerring described four, and some authors have mentioned a larger number; but their descriptions have not been confirmed by later research. Of the two muscles generally recognised, one is attached to the malleus, and the other to the stapes.

The *tensor tympani* (fig. 381, *tt*), is the larger of these muscles. It consists of a tapering fleshy part, about half an inch in length, and a slender tendon. The muscular fibres arise from the cartilaginous end of the Eustachian tube and the adjoining surface of the sphenoid bone, and from the sides of the canal in which the muscle lies and in which it is conducted backwards to the cavity of the tympanum. Immediately in front of the fenestra ovalis the tendon of the muscle bends at nearly a right angle over the end of the processus cochleariformis as round a

pulley, and, contained in a fibrous sheath, passes outwards, to be inserted into the inner part of the handle of the malleus, close to its root.

The *stapedius* is a very distinct muscle, but is hid within the bone, being lodged in the descending part of the aqueductus Fallopii and in the hollow of the pyramid. The tendon issues from the aperture at the apex of that little elevation (fig. 374), and passing forwards, surrounded by a fibrous sheath, is inserted into the neck of the stapes posteriorly, close to the articulation of that bone with the lenticular process of the incus.

A very slender spine of bone has been found occasionally in the tendon of the stapedius in man : and a similar piece of bone, though of a rounder shape, exists constantly in the horse, the ox, and other animals.

Fig. 382.

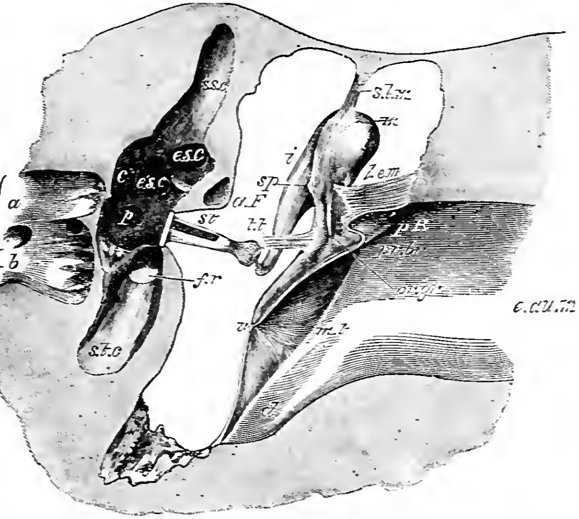


Fig. 382.—Profile view of the left membrana tympani and auditory ossicles from before and somewhat from above. Magnified four times. (E. A. S.)

The anterior half of the membrane has been cut away by an oblique slice. *m*, head of the malleus ; *sp*, spur-like projection of the lower border of its articular surface ; *pr. br*, its short process ; *pr. gr*, root of processus gracilis, cut ; *s.l.m*, suspensory ligament of the malleus ; *l.e.m*, its external ligament : *t.t*, tendon of the tensor tympani, cut : *i*, incus, its long process ; *st*, stapes in fenestra ovalis : *e.au.m*, external auditory meatus ; *p.R*, notch of Rivini ; *m.t*, membrana tympani : *u*, its most depressed point or umbo ; *d*, declivity at the extremity of the external meatus ; *i.au.m*, internal auditory meatus ; *a* and *b*, its upper and lower divisions for the corresponding parts of the auditory nerve : *n.p*, canal for the nerve to the ampulla of the posterior semicircular canal : *s.s.c*, ampullary end of the superior canal ; *p*, ampullary opening of the posterior canal : *c*, common aperture of the superior and posterior canals ; *e.s.c*, ampullary, and *e'.s.c*, non-ampullary end of the external canal ; *s.t.c*, scala tympani cochleæ ; *f.r*, fenestra rotunda, closed by its membrane ; *a.F*, aqueduct of Fallopius.

Movements of the auditory ossicles.—The malleus and incus move together round an axis extending backwards from the attachment of the malleus by its anterior ligaments to the attachment of the short process of the incus posteriorly. The handle of the malleus follows all the movements of the membrana tympani, and when the membrane is impelled inwards, the incus, moving inwards along with the malleus, pushes the stapes inwards towards the internal ear. In this movement the head of the stapes is slightly raised as well as pressed inwards, and the upper margin of its base moves more than the lower.

But the cavity of the inner ear is full of liquid; and its walls are unyielding, except at the fenestra rotunda; when, therefore, the stapes is pushed inwards, the secondary membrane of the tympanum, which blocks up the fenestra rotunda, must be bulged outwards. When the membrana tympani returns to its original condition these movements are reversed. That the movement inwards of the incus must closely accompany that of the malleus, is necessitated by the fact that the lower margin of its articular surface has a well marked projection which catches against the prominent border of the articular surface of the malleus (fig. 382, *sp*). If, however, in consequence of increase of tension of the air in the tympanum, the malleus should be moved too freely outwards, the incus need not follow that movement to its full extent, but may merely glide over the smooth adjoining surface of the malleus, and thus the danger that there would otherwise be of forcibly dragging out the stapes from the fenestra ovalis is avoided.

The tensor tympani muscle, being attached near the base of the manubrium of the malleus, draws the whole bone and the membrane inwards, tightening the latter. Its action is opposed by the strong external ligament of the malleus. The tensor tympani exerts but little rotating action upon the malleus. The action of the stapedius muscle is obviously to draw the head of the stapes backwards, in doing which the hinder end of the base of that bone will be pressed against the margin of the fenestra ovalis, while the fore part will be withdrawn from the fenestra.

The lining membrane of the tympanum.—The mucous membrane of the tympanum is continuous with that of the pharynx through the Eustachian tube, and is further prolonged from the tympanum backwards into the mastoid cells. Two folds which cross the breadth of the cavity descend from the part of the membrane which lines the roof. The anterior fold turns round the tendon of the tensor tympani muscle; the posterior fold passes round the stapes. The malleus and incus are invested by the lining of the outer wall of the cavity; which forms also prominent folds in front of and behind the neck of the malleus; these folds separating off a small pouch-like corner of the tympanic cavity corresponding with the situation of the membrana flaccida. Various other smaller folds are met with, and they for the most part contain strands of fibrous tissue and sometimes osseous spicules.

The mucous membrane which lines the cartilaginous part of the Eustachian tube resembles much the membrane of the pharynx, with which it is immediately continuous; it is thick and vascular, is covered by ciliated epithelium, and is provided with many simple mucous glands which pour out a thick secretion: in the osseous part of the tube, however, the membrane becomes gradually thinner. In the tympanum and the mastoid cells the mucous membrane is paler, thinner, and less vascular, and secretes a less viscid, somewhat yellow fluid. Between it and the periosteum is a network of fibrous bundles, which are here and there raised above the general surface, causing corresponding projections of the mucous membrane. In various places on the interlacing bundles, peculiar swellings occur of various sizes, which appear to be caused by the superaddition of concentrically arranged fibres upon the smaller bundles, and produce an appearance similar to that of miniature Pacinian corpuscles (Politzer, Kessel). The epithelium in the tympanic cavity is in part columnar and ciliated, but the roof, the promontory, the ossicula, and the membrana, are covered with a simple layer of flattened non-ciliated cells (v. Troeltsch).

Vessels and Nerves of the Tympanum.—The arteries of the tympanum, though very small, are numerous, and are derived from branches of the external, and from the internal carotid.

The fore part of the cavity is supplied chiefly by the *tympanic branch* of the internal maxillary, which enters by the fissure of Glaser. The back part of the cavity including the mastoid cells, receives its arteries from the *stylo-mastoid branch* of the posterior auricular artery, which is conducted to the tympanum by the aqueduct of Fallopius. These two arteries form by their anastomosis a vascular circle round the margin of the membrana tympani. The smaller arteries of the tympanum are, the *petrosal branch* of the middle meningeal, which enters through the *hiatus Fallopii*, and branches through the bone *from the internal carotid* artery, furnished from that vessel whilst in the carotid canal.

The **veins** of the tympanum empty their contents into the superior petrosal sinus and the temporo-maxillary vein.

Nerves.—The tympanum contains numerous nerves; for, besides those which supply the parts of the middle ear itself, there are several which serve merely to connect nerves of different origin.

The lining membrane of the tympanum is supplied by filaments from the tympanic plexus, which occupies the shallow grooves on the inner wall of the cavity, particularly on the surface of the promontory (fig. 375).

This plexus (fig. 383) is formed by 1st, the nerve of Jacobson from the petrous ganglion of the glosso-pharyngeal; 2nd, a filament connecting the nerve of Jacobson with the carotid plexus of the sympathetic; 3rd, a branch which joins the great superficial petrosal nerve; 4th and lastly, the small superficial petrosal nerve, passing to the otic ganglion.

Numerous ganglion cells are found both in the uniting cords and also at the points of junction of the plexus.

Fig. 383.

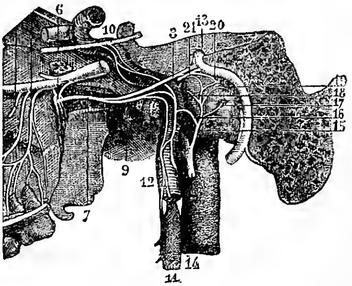


Fig. 383.—View of the tympanic plexus of Nerves (from Sappey, after Hirschfeld and Leveillé).

6, spheno-palatine ganglion; 7, Vidian nerve; 8, great superficial petrosal nerve; 9, carotid branch of the Vidian nerve; 10, part of the sixth nerve connected by twigs with the sympathetic; 11, superior cervical ganglion of the sympathetic; 12, carotid branch; 13, facial nerve; 14, glosso-pharyngeal nerve; 15, nerve of Jacobson; 16, its twig to the sympathetic; 17, filament to the fenestra rotunda; 18, filament to the Eustachian tube; 19, filament to the fenestra ovalis; 20, small superficial petrosal nerve; 21, filament joining large superficial petrosal.

The nerve of Jacobson (fig. 383, 15) enters the tympanum by a small foramen near its floor, which forms the upper end of a short canal in the petrous portion of the temporal bone, beginning at the base of the skull between the carotid foramen and the jugular fossa. The nerve from the carotid plexus is above and in front of this, and passes through the bone directly from the carotid canal. The branch to the great superficial petrosal nerve (fig. 383, 21) is lodged in a canal which opens on the inner wall of the tympanum in front of the fenestra ovalis. The small superficial petrosal nerve also leaves at the fore part of the cavity beneath the canal for the tensor tympani.

The tensor tympani muscle obtains its nerve from the otic ganglion; and the stapedius receives filaments from the facial nerve.

The *chorda tympani* arising from the facial near the lower end of the aqueduct of Fallopius, takes a recurrent course to the tympanum, which it enters by an aperture in the posterior wall just below the level of the pyramid. From this place it passes with a slight curve across the cavity near the outer boundary, and crossing successively the posterior part of the membrana tympani, the handle of the malleus near its neck, and the processus gracilis of the same bone, finally enters a small canal in the bone close to the Glaserian fissure (fig. 374, *ch*). It is invested by the fold of the lining membrane already mentioned as occurring in this situation.

THE INTERNAL EAR, OR LABYRINTH.

The inner, essential part of the organ of hearing, is contained in the petrous portion of the temporal bone. It consists of a complex cavity—the osseous labyrinth—hollowed out of the bone, and containing the membranous labyrinth.

The *osseous labyrinth* is incompletely divided into three parts, named the vestibule (fig. 384, 1), the semicircular canals (3, 4, 5), and the cochlea (6, 7). They are lined throughout by a thin periosteal membrane, within which there is a clear fluid named perilymph, or liquor Cotunnii.

The *membranous labyrinth* being distinctly smaller than the bony labyrinth, a space is left between the two, occupied by the perilymph just referred to. The membranous structure is lined throughout by epithelium, and at certain parts receives branches of the auditory nerve. It contains a fluid named the endolymph.

THE OSSEOUS LABYRINTH.

The **vestibule** forms a central chamber of the labyrinth, which communicates in front with the cochlea, and behind with the semicircular canals. It is irregularly ovoidal in shape, measuring about $\frac{1}{5}$th of an inch from before back but slightly less from without inwards.

The outer wall, which separates it from the cavity of the tympanum, is perforated by the fenestra ovalis, which in the recent state is closed by the base of the stapes.

At the fore part of the inner wall is a small round pit, the *fovea hemispherica* (fig. 385, 2), pierced with many minute holes, which serve to transmit branches of the auditory nerve from the internal auditory meatus. This fossa is limited behind by a vertical ridge named *crista vestibuli.* Behind the crest is the small oblique opening of a canal, the *aqueduct of the vestibule* (fig. 385, 4), which extends to the posterior surface of the petrous bone.

In the roof is an oval depression, placed somewhat transversely, *fovea hemi-elliptica* (fig. 385, 1), the inner part of which is separated by the crest from the hemispherical fossa.

At the back part of the vestibule are five round apertures, leading into the semicircular canals: and at the lower and fore part of the cavity is a larger opening, which communicates with the scala vestibuli of the cochlea.

The **semicircular canals** are three tubes, situated above and behind the vestibule, into which they open by five apertures, the contiguous ends of two of the canals being joined. They are unequal in length, but each tube is bent so as to form about two-thirds of a circle; and is moreover dilated at one end, the enlargement being known as the *ampulla.* The canals are compressed laterally, and measure about $\frac{1}{20}$th of an inch across; but the ampulla has a diameter of $\frac{1}{10}$th of an inch.

The canals differ from one another in direction, in length, and in position with regard to the vestibule. The *superior* semicircular canal (fig. 384, 3, fig. 385, 5) is nearly vertical and lies transversely; it rises higher than any other part of the labyrinth, and its place is indicated by a smooth arched projection on the upper surface of the petrous bone. The ampullary end of this canal is the external and anterior, and opens by a distinct orifice into the upper part of the vestibule; whilst the opposite extremity joins the non-dilated end of the posterior semicircular canal, and opens by a common aperture with it into the back part

of the vestibule (fig. 385, 3). The *posterior* semicircular canal (fig. 384, 5, fig. 385, 6), also nearly vertical, lies antero-posteriorly, but both it and

Fig. 384.

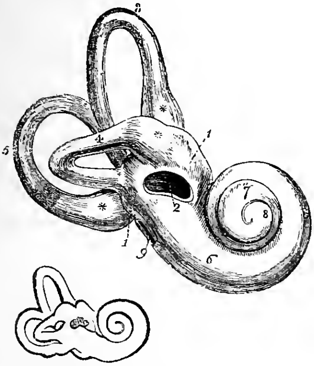


Fig. 385.

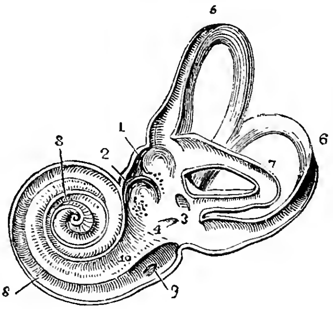


Fig. 384.—Right bony labyrinth, viewed from the outer side (after Sömmerring). $\frac{2\frac{1}{2}}{1}$

The specimen here represented is prepared by separating piecemeal the looser substance of the petrous bone from the dense walls which immediately enclose the labyrinth. 1, the vestibule; 2, fenestra ovalis; 3, superior semicircular canal; 4, horizontal or external canal; 5, posterior canal; * * *, ampullæ of the semicircular canals; 6, first turn of the cochlea; 7, second turn; 8, apex; 9, fenestra rotunda. The smaller figure in outline below shows the natural size.

Fig. 385.—View of the interior of the left labyrinth (from Sömmerring). $\frac{2\frac{1}{2}}{1}$

The bony wall of the labyrinth is removed superiorly and externally. 1, fovea hemi-elliptica; 2, fovea hemispherica; 3, common opening of the superior and posterior semicircular canals; 4, opening of the aqueduct of the vestibule; 5, the superior, 6, the posterior, and 7, the external semicircular canals; 8, spiral tube of the cochlea (scala tympani); 9, opening of the aqueduct of the cochlea; 10, placed on the lamina spiralis in the scala vestibuli.

the superior canal incline towards one another at their inner ends. The posterior is the longest of the three tubes: its ampullary end is placed

Fig. 386.

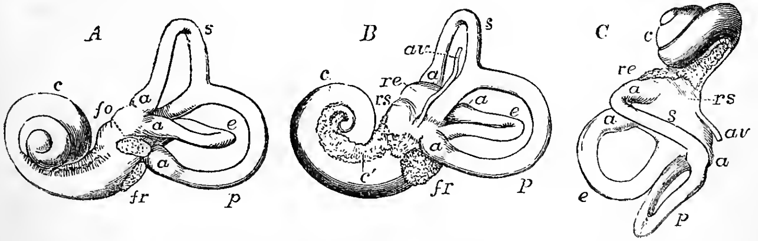


Fig. 386.—Views of a cast of the interior of the labyrinth (from Henle). $\frac{2}{1}$

Such casts may easily be made in fusible metal, and give a very correct view of the form of the different parts of the labyrinthic cavity. A, view of the left labyrinth from the outer side; B, the right labyrinth from the inner side; C, the left labyrinth from above; *s*, the superior, *p*, the posterior, and *e*, the external semicircular canals; *a*, their several ampullæ; *r e*, fovea hemi-elliptica of the vestibule; *r s*, fovea hemispherica; *a v*, aqueduct of the vestibule; *f o*, fenestra ovalis; *f r*, fenestra rotunda; *c*, the coiled tube of the cochlea; *c′*, the tractus foraminosus spiralis.

at the lower and back part of the vestibule; and the opposite end terminates in the common canal above described. The *external* semicircular canal (fig. 384, 4; fig. 385, 7) arches *horizontally* outwards, and opens by two distinct orifices into the upper and back part of the vestibule. The canal is shorter than either of the other two: its ampulla is at the outer end, above the fenestra ovalis.

The **cochlea** (fig. 384, 6, 7, 8), when cleared of the surrounding less dense bony substance in which it lies embedded, appears in the form of a blunt cone, the base of which is turned towards the internal auditory meatus, whilst the apex is directed outwards, with an inclination forwards and downwards, and is close to the canal for the tensor tympani muscle. It measures about $\frac{1}{4}$ of an inch in length, and the same in breadth at the base.

Fig. 387.

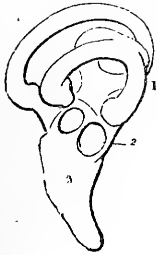


Fig. 387.—Osseous Labyrinth of the barn owl (strix flammea) (from Breschet). $\frac{4}{1}$

1, semicircular canals; 2, vestibule; 3, cochlea in the form of a short straight tube.

It consists of a gradually tapering spiral tube, the inner wall of which is formed by a central column, or *modiolus* (fig. 388, 1), around which it winds. It is partially divided along its whole extent by a spiral lamina (2), projecting into it from the modiolus. From this osseous spiral lamina membranous structures are in the recent condition stretched across to the outer wall of the tube, and thus completely separate two passages or *scalæ*, one on each side of the spiral lamina, which communicate one with the other only by a small opening, named *helicotrema*, placed at the apex of the cochlea.

That the cochlea is justly to be considered as an elongated tube, coiled spirally on the modiolus, is illustrated by the simple pouch-like form of the rudimentary cochlea of birds (fig. 387) as well as by the history of its development.

The *spiral osseous canal* is nearly $1\frac{1}{2}$ inch long, and about $\frac{1}{10}$ inch in diameter at the commencement, where it is widest. From this point the canal makes $2\frac{1}{2}$ turns round the central pillar (from left to right in the right ear, and in the opposite direction in the left ear, supposing the

Fig. 388.

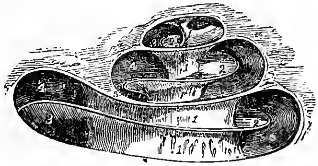


Fig. 389.

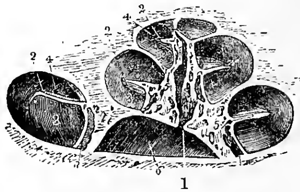


Fig. 388.—Diagrammatic view of the osseous cochlea laid open. $\frac{5}{1}$

1, modiolus or central pillar; 2, placed on three turns of the lamina spiralis; 3, scala tympani; 4, scala vestibuli.

Fig. 389.—View of the osseus cochlea divided through the middle. (from Arnold). $\frac{5}{1}$

1, central canal of the modiolus; 2, lamina spiralis ossea; 3, scala tympani; 4, scala vestibuli; 5, porous substance of the modiolus; 6, end of the internal auditory meatus.

cochlea viewed from the base), and ends by an arched and closed extremity called the *cupola*, which forms the summit of the cochlea. The first coil, having by far the most extensive curve and being the largest portion of the tube, nearly hides the second from view; and, bulging somewhat into the tympanum, forms the round elevation on the inner wall of that cavity called the promontory.

The *modiolus* (columella cochleæ), the central pillar or axis of the cochlea, is much the thickest within the first turn of the tube, rapidly diminishing in size in the succeeding parts. Its central part is spongy as far as the last half coil, and is pierced by many small canals, for the passage of the nerves and vessels to the spiral lamina; one of these canals, larger than the rest, *central canal of the modiolus*, runs from the base through the centre of the modiolus (fig. 389, 1).

The *osseous spiral lamina* is a thin, flat plate, growing from the modiolus, and projecting into the spiral tube, so as to divide it partly into two. It does not reach farther than about half-way towards the outer wall of the spiral tube. Close to the apex of the cochlea, it ends in a hooklike process (*hamulus*), which partly bounds the helicotrema.

The lamina is thin and dense at its free edge; but nearer the modiolus its internal structure is more open and spongy, and contains numerous small canals for vessels and nerves, continuous with, but running at right angles to, the canals in the modiolus. Winding round the modiolus, in the base of the spiral lamina, is a small canal, named the *spiral canal of the modiolus*.

The *scala tympani* (fig. 388, 3), the portion of the tube on the basal side of the lamina spiralis, commences at the fenestra rotunda, where in the recent state it is separated from the tympanum by the secondary membrane of the tympanum. Close to its commencement is the orifice of a small canal (*aqueductus cochleæ*, fig. 385, 9), which extends downwards and inwards through the substance of the petrous bone to the jugular fossa, to which it transmits a small vein. There is also a communication through it between the scala tympani and the subarachnoid space. The *scala vestibuli* (fig. 388, 4) is rather narrower than the scala tympani in the first turn of the cochlea; it commences from the cavity of the vestibule, and communicates, as already described, with the scala tympani at the apex of the modiolus.

THE MEMBRANOUS LABYRINTH.

Within the osseous labyrinth, and separated in most parts from its lining membrane by the perilymph, membranous structures exist in which the ultimate ramifications of the auditory nerve are spread. In the vestibule and semicircular canals these structures have a general resemblance in form to the complicated cavity in which they are contained. They do not, however, lie loose within the osseous cavity, but along the convex border of the canals, and at the places of entrance of the nerves into the vestibule and ampullæ are fixed to its wall. In the cochlea the membranous structures complete the septum between the scalæ already mentioned, and enclose an intermediate passage, the membranous *canal of the cochlea*. As before stated, the liquid contained within the membranous labyrinth is distinguished as *endolymph*.

The cavity which contains the perilymph communicates through the sheath of the auditory nerve with both the subdural and subarachnoid spaces.

VESTIBULE.—Within the *osseous* vestibule are two membranous sacs,

the one of which, termed the *utricle*, is connected with the semicircular canals, whilst the other, the *saccule*, is connected with the cochlea. These two sacs although in close contact do not open directly into one another although they are in indirect communication, in a manner presently to be explained.

The larger of the two sacs, the *common sinus* or **utricle** (fig. 390, *u*), is of an oblong form, slightly flattened from without inwards. It is lodged in the upper and back part of the vestibule, occupying the fovea hemi-elliptica and the space immediately below this. Opposite the crista vestibuli several small branches of the auditory nerve enter from the foramina in the bone; and here the walls of the common sinus are thicker and more opaque than elsewhere (*macula acustica*). A small mass of calcareous particles (*otoliths* or *otoconia*) lies within the sac, attached to its walls at this place. These otoliths are crystals of carbonate of lime, rhombic, octahedral, or six-sided, often pointed at their extremities.

Fig. 390.

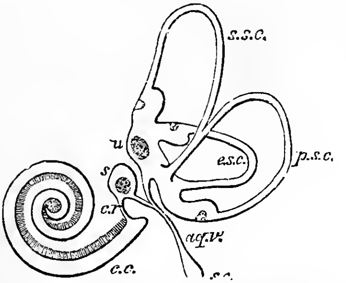


Fig. 390.—PLAN OF THE RIGHT MEMBRANOUS LABYRINTH VIEWED FROM THE MESIAL ASPECT (E A.S.) $2\frac{1}{2}$.

u, utricle, with its macula and the three semicircular canals with their ampullæ; *s*, saccule; *aq. v.* aqueductus vestibuli; *s. e.* saccus endolymphaticus; *c. r.* canalis reuniens; *c. c.* canal of the cochlea.

The ends of all the membranous semicircular canals open into the utricle.

The small vestibular vesicle, the **saccule** (fig. 390, *s*), is more nearly spherical than the common sinus, but, like it, is somewhat flattened. The saccule is situated in the lower and fore part of the cavity of the osseous vestibule, close to the opening from the scala vestibuli of the cochlea, and is received into the hollow of the fovea hemispherica, from the bottom of which many branches of nerve enter it, and here there is a similar macula in its wall. It also contains a small mass of otoliths.

Fig. 391.

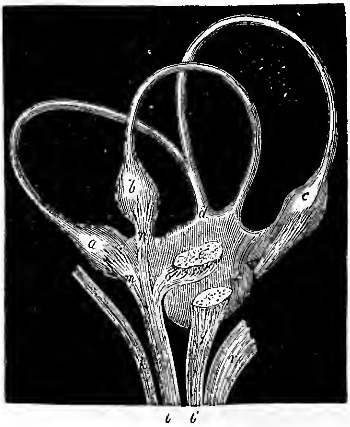


Fig. 391.—MEMBRANOUS LABYRINTH AND NERVOUS TWIGS DETACHED, MAGNIFIED (Breschet).

k, facial nerve in the meatus auditorius internus; *l*, anterior division of the auditory nerve giving branches, *o*, *m*, *n*, to the utricle and the ampullæ of the superior and external canals; *l′*, vestibular division of the auditory nerve, giving a branch, *q*, to the saccule, another to the posterior ampulla, *q*, and a third (*r*) to the cochlea, *r*; *a*, *b*, *c*, ampullæ of the superior, external, and posterior semicircular canals respectively; *d*, the united part of the superior and posterior canals; *e*, the macula of the utricle; *f*, the saccule.

The saccule is connected with the membranous canal of the cochlea by means of a short narrow canal, the *canalis reuniens* of Hensen (*c. r.*). There is also a minute canal, lined with epithelium, which passes from the utricle along the aqueductus vestibuli to end blindly in a dilated extremity (saccus endo-lymphaticus (*s.e.*)) on the posterior surface of the petrous bone just below the orifice of the aqueduct and lying in the tissue of the dura mater. This canal is joined near its origin by a small tube from the saccule, so that in this way the cavity of the saccule is brought into communication with that of the utricle (Boettcher).

SEMICIRCULAR CANALS.—The **membranous semicircular canals** are from one-third to one-fifth the diameter of the osseous tubes in which they are lodged, and are dilated into ampullæ within the ampullary enlargements of those tubes. In section they are oval or somewhat elliptical (fig. 392). At the ampullæ they are thicker and less translucent than in the rest of their extent, and nearly fill their bony cases. That part of each which is towards the concavity of the semicircle of the canal is free; whilst the opposite portion is fixed to the wall of the bony canal; in the ampulla this part is flattened and receives branches of nerves and blood-vessels, and on its inner surface is a transverse projection, (*crista acustica*) which partly divides the cavity into two.

Auditory nerve.—Within the internal auditory meatus the auditory nerve divides into two branches, which, broken up into minute filaments, pass through the perforations of the cribriform plate which separates the meatus from the internal ear, and are distributed respectively to the cochlea and vestibule. In both branches, as well as in the trunk, there are numerous nerve-cells. The superior division (fig. 391, *l*), which is at first also anterior in position and is separated by a crest of bone from the other division below it, gives off three branches, which proceed respectively to the utricle and the ampullæ of the superior and external semicircular canals, entering the vestibular cavity in a group along the crista vestibuli. The inferior division on the other hand (*l′*), which is at first behind as well as below the vestibular division, gives off, besides the numerous fibres which enter the cochlea by the tractus foraminulentus, a branch for the saccule—which enters the vestibule by a small group of foramina, which open at the bottom of the fovea hemispherica—and the branch for the posterior semicircular canal which is long and slender, and traverses a small passage in the bone behind the foramina for the nerve of the sacculus. The nerves of the ampullæ enter the flattened or least prominent side of the ampullæ, where they each form a forked swelling, which corresponds with the crista acustica, in the interior of the dilatation. No nerves have been found extending to any other parts of the semicircular canals.

Vessels of the labyrinth.—The *internal auditory artery*, a branch of the basilar, accompanies the auditory nerve in the internal auditory meatus, and divides into branches for the vestibule and cochlea. Those of the vestibule supply the membranous labyrinth and the endosteum, and small vessels ensheathed by fibrous tissue pass across the cavity containing the perilymph. The blood is chiefly collected into the internal auditory veins which accompany the artery and open into the inferior petrosal or the transverse sinus, but some is conveyed to the inferior petrosal sinus by fine veins in the aqueductus vestibuli.

Structure of the membranous labyrinth.—Three layers can be distinguished in the membranous walls of the semicircular canals, an

Fig. 392.

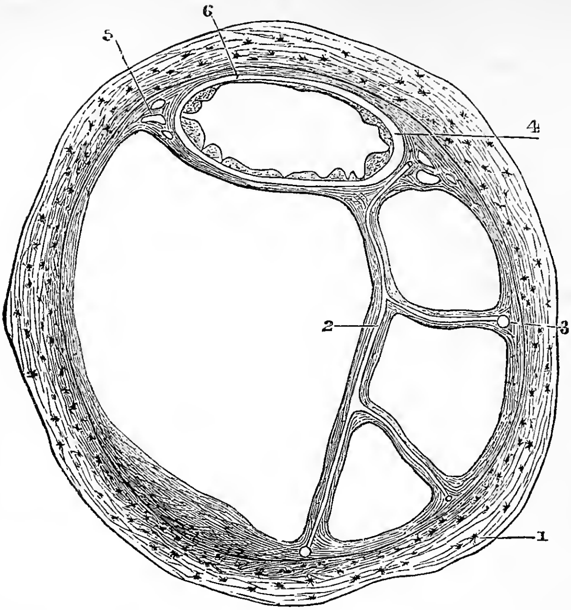


Fig. 392.—Section of one of the human semicircular canals (Rüdinger). Magnified.

1, osseous wall; 2, fibrous bands with included blood-vessels, united at 3 with the periosteum; 4, membranous canal with its three layers; 5, short fibrous bands (with intervening spaces) uniting the membranous canal firmly to the periosteum; 6, union of its outermost layer with the periosteum.

Fig. 393.

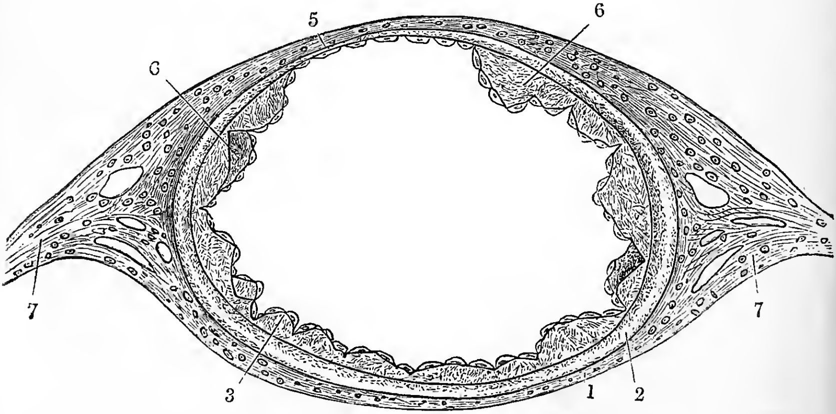


Fig. 393.—Section of membranous semicircular canal, much magnified (Rüdinger).

1, outer fibrous layer; 2, tunica propria; 3, 6, papilliform projections with epithelial covering; 5, fixed side of the canal, with very thin tunica propria without papillæ; 7, fibrous bands passing to periosteum.

outer fibrous stratum, an inner epithelial lining, and between the two a tunica propria. These layers are not of equal thickness throughout, for along the side which is in contact with and supported by the bone (fig. 392, 6), they are thinner than at the rest of the circumference, where they lie free and are bathed by the perilymph. The difference in thickness affects the fibrous layer and the tunica propria only, for the epithelium forms throughout a lining of simple flattened cells.

The *fibrous layer* (fig. 392, 1), which contains some irregular pigment-cells, is apparently composed of ordinary fibrous tissue, similar to that of the periosteum, with which it becomes continuous at the parts where the two structures are in contact. It is especially developed at the ends of the oval section, whence well-marked bands of fibrous tissue pass to the periosteum (fig. 392, 7). More delicate bands of fibrous tissue traverse the perilymph to become connected with the periosteum of the opposite wall of the canal (fig. 392, 2). Both along these bands and also more directly from the contiguous periosteum, numerous small blood-vessels pass into the fibrous layer and there break up into a coarse capillary network, the branches of which do not, in man, pass into the tunica propria.

The *tunica propria* is a clear membranous structure continuous around the whole tube, although thinning off very much opposite the part where the membranous canal is in contact with the bone (fig. 393, 5). Externally it is not very distinctly marked off from the fibrous coat: internally it has a number of papilliform eminences (fig. 393, 3, 6,) which project into the interior of the canal except at the thinnest part (Rüdinger).

The *epithelial lining* takes the form of a complete layer of flattened cells, which in the human semicircular canals are of the same nature throughout.

In many of the lower animals—birds and fishes—some of these lining cells are columnar, while in one species of fish, (Salmo hucho), as described by Rüdinger, a tract along the whole length of each canal becomes developed into two rows of rounded cells, from each of which a long filament extends to the wall of the canal in a direction transverse to the axis.

The meaning of these modifications of structure is unknown. No nerves have hitherto been seen proceeding to the parts in question; but they apparently represent the much more developed peculiarly modified epithelium which, as we shall immediately see, is found in the ampullæ and in the saccule and utricle opposite the parts where the branches of the auditory nerve enter, and which receives the ultimate terminations of those nerves.

The ampullæ, as well as the saccule and utricle, agree generally in structure with the semicircular canals: but at the part where they are connected to the osseous wall the fibrous outer layer is looser, and the tunica propria is much thickened, and in the ampullæ projects into the cavity as the *septum transversum* or *crista acustica,* before mentioned. Through the substance of this thickening the nerve-fibres pass to the edge of the ridge, and over it the epithelium is of an elongated columnar form (fig. 394), and is surmounted by long, conical, gradually tapering filaments (auditory hairs (*h*)), which project stiffly into the cavity. These hairs are borne by the columnar epithelium-cells, a single hair projecting from each cell, but under the influence of reagents they are apt to become broken near the base, and this splits up into fine fibrils which then appear as a bunch of cilium-like filaments attached to the

free border of the cell (fig. 395, *h, h'*). The columnar cells, or *hair cells*, do not extend down to the basement membrane, but terminate short of this in a somewhat pointed extremity. They are directly connected by this extremity with branches of the nerve-fibres which penetrate into the epithelium (fig. 395, *n*). This connection has been described by Retzius in reptiles and there is little doubt it obtains in all vertebrates.

Fig. 394.

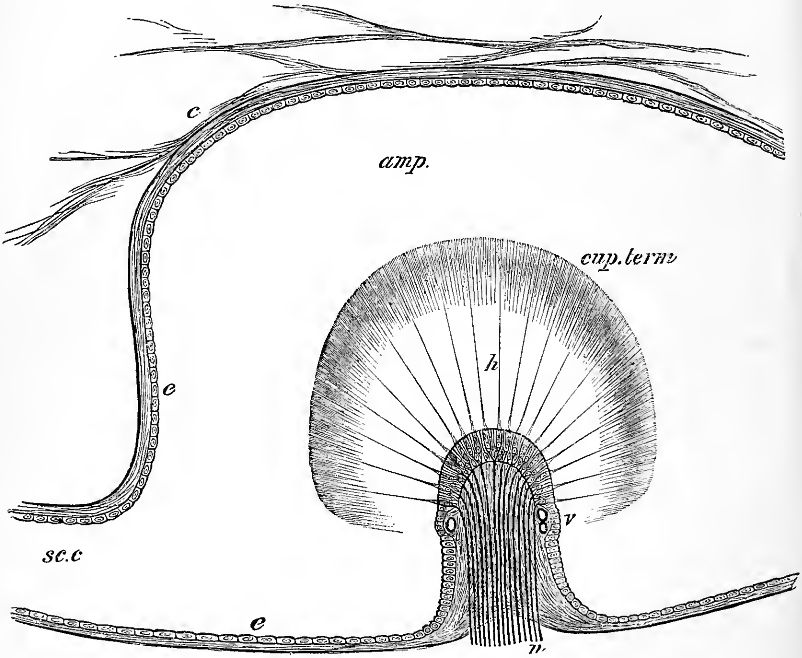


Fig. 394.—Longitudinal section of an ampulla through the crista acustica. Semi-diagrammatic (E. A. S.).

amp, cavity of the ampulla ; *sc. c*, semicircular canal opening out of it ; *c*, connective tissue attached to the wall of the membranous ampulla and traversing the perilymph ; *e e*, flattened epithelium of ampulla ; *h*, auditory hairs projecting from the columnar cells of the auditory epithelium into the cupula, *cup. term.* ; *v*, a vascula stria marking the limit of the auditory epithelium on the crista ; *n*, nerve-fibres entering the base of the crista and passing into the columnar cells.

Between and beneath the columnar cells other cells are met with of a different character. They take the form of long and comparatively rigid fibres (*fibre-cells* of Retzius) which extend through the whole thickness of the epithelium, and are provided at one part of their course with a nucleated enlargement. This is always placed below the columnar cells, and in many it is close to the central end of the fibre. The fibres, which are probably sustentacular in function, like the fibres of Müller in the retina, expand slightly as they approach the free surface, and appear to become attached to a cuticular structure which encloses the ends of the hair-cells and is thus comparable to the reticular lamina of the cochlea (Urban Pritchard). On the other hand the fibres are set by their central ends upon a limiting membrane which bounds

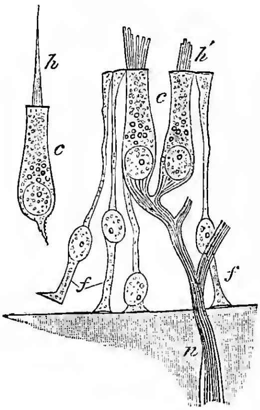
the epithelium next to the tunica propria, and which appears in section as a fine but well-marked line.

The limits of the auditory epithelium at the sides of the crest appear to be marked, at least in the human ampullæ, by a prominent vascular stria (fig. 394, *v*) (E.A.S.).

Fig. 395.—Auditory epithelium from the macula acustica of the saccule of a reptile (Retzius). Highly magnified.

c c, columnar cells ; *f f*, fibre-cells ; *n*, nerve-fibre, losing its medullary sheath and passing to terminate in the columnar auditory cells ; *h*, auditory hair ; *h'*, base of auditory hairs, split up into fibrils.

Fig. 395.



The auditory hairs were first noticed by Max Schultze, and were believed at first to be connected with the elongated cells and not with those of a columnar shape. Their true relations were pointed out by Retzius, and in this matter my own observations, in the fish and in man, entirely coincide with his. When the cells are isolated after preservation in osmic acid, the separated columnar cells are alone surmounted by auditory hairs, whereas the elongated intermediate cells are not provided with auditory filaments. Urban Pritchard has rightly figured hese sustentacular cells in the cat as expanding into the so-called reticular lamina, but his description of their continuity with auditory filaments is not borne out by subsequent investigations. It is worthy of note that the auditory hairs do not project freely into the endolymph of the ampulla, but into a soft material which takes a dome-like shape (cupula terminalis, Lang), and appears to possess an indistinctly fibrillar structure. It is not possible therefore to suppose that the hairs can be set in vibration singly, but whatever movements are communicated to the endolymph, must affect the whole cupula and all the hairs embedded in it (E.A.S.).

The foregoing description, although referring more particularly to the characters of the epithelium and mode of nerve-distribution in the cristæ acusticæ of the ampullæ, is equally applicable to the maculæ acusticæ of the saccule and utricle. The nerves which are supplied to the maculæ seem, however, to spread out more than those to the ampullæ. As before mentioned, both saccule and utricle contain in their cavity and lying in contact with the nerve-epithelium a little mass of otoliths, which, however, do not float free in the fluid, but appear imbedded in a soft matrix which again may be enclosed in a delicate cuticular investment. Otoliths are also found scattered here and there in the ampullæ and semicircular canals.

Cochlea.—The **membranous cochlea** resembles the membranous semicircular canals just described in consisting of a tube, lined by epithelium and containing endolymph, partly surrounded by a clear space containing perilymph, but it differs from them both in shape and n the modifications presented by its epithelial lining. In macerated specimens, the two parts into which the osseous tube of the cochlea is divided are, it will be remembered, only imperfectly separated by the osseous spiral lamina which projects from the columella ; but in the fresh specimen the tube is separated completely into three distinct parts by means of two membranes, which extend along its whole length (figs. 396 to 398). In the first place the lamina spiralis is directly prolonged by a comparatively strong, well-marked membrane, the *basilar membrane*

(fig. 398, *b*), which stretches straight across to the outer wall of the cochlea, and is here connected to an inward projection of the lining periosteum and sub-periosteal tissue known as the *spiral ligament* (*lsp*). The basilar membrane thus helps to complete the upper* limit of the

Fig. 396.

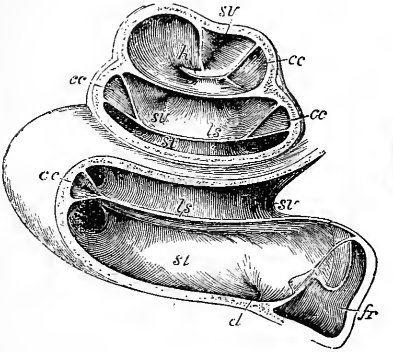


Fig. 397.

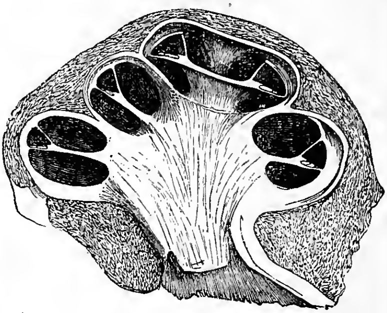


Fig. 396.—Left cochlea of a child some weeks old (Reichert). $\frac{6}{1}$

The drawing was taken from a specimen which had been preserved in alcohol, and was afterwards dried; a section is made so as to show the lamina spiralis, scalæ, and cochlear canal in each of the three coils: the membranous spiral lamina is preserved, but the appearances connected with the organ of Corti, &c., have been lost from drying. *f r*, fenestra rotunda with its membrane; *s t*, scala tympani; *s v*, scala vestibuli; *l s*, lamina spiralis; *h*, hamulus; *c c*, canalis cochleæ; *d*, opening of the aqueductus cochleæ.

Fig. 397.—Vertical section of the cochlea of a fœtal calf (Kölliker). $\frac{6}{1}$

In this specimen the external wall was ossified, but the modiolus and spiral lamina was still cartilaginous; the section shows in each part of the cochlear tube the two scalæ with the intermediate canalis cochleæ and lamina spiralis.

scala tympani (*ST*), but does not properly speaking enter into the lower boundary of the scala vestibuli, for a second, much more delicate mem-

Fig. 398.

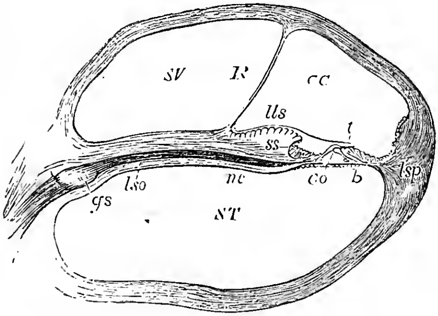


Fig. 398.—Section through one of the coils of the cochlea, diagrammatic (altered from Henle). $\frac{30}{1}$

S T, scala tympani; *S V*, scala vestibuli; *C C*, canalis cochleæ; *R*, membrane of Reissner forming its vestibular wall; *l s o*, lamina spiralis ossea; *l l s*, limbus laminæ spiralis; *s s*, sulcus spiralis; *n c*, cochlear nerve; *g s*, ganglion spirale; *t*, membrana tectoria; *b*, membrana basilaris; *C o*, rods of Corti; *l s p*, ligamentum spirale.

* To avoid repetition it may here be stated that for convenience sake the cochlea is considered in the present description as having its larger part or base lowermost, and the domed extremity uppermost, although of course this is far from being the relative position of the parts whilst within the body. Moreover, parts nearer the columella are spoken of as *inner*; parts nearer the external wall as *outer*.

brane, known as the membrane of Reissner (*R*) passes from the upper part of the lamina a little distance from its end, and stretches obliquely upwards and outwards, also to become connected with the lining periosteum. The oblique direction of the membrane of Reissner causes a triangular space to be shut off between it and the basilar membrane, which is bounded externally by the outer osseous wall of the cochlea lined by periosteum : and this space, extending throughout the whole length of the osseous tube, and lined throughout by an epithelium variously modified in different parts, is known distinctively as the *canal of the cochlea, canalis membranaceus,* or *ductus cochlearis* (figs. 397, 398, *CC*, fig. 400, *DC*). It terminates in a blind pointed extremity at the apex, and another at the base. That at the apex, extending beyond the hamulus, is fixed to the wall of the cupola, and partly bounds the helicotrema ; that at the base fits into the angle at the commencement of the osseous spiral lamina in front of the floor of the vestibule. Near to this blind extremity the canal of the cochlea receives a small canal, lined with epithelium, *canalis reuniens* (Hensen), which is continued from the saccule of the vestibule like the neck of a flask, and enters the canal of the cochlea abruptly nearly at a right angle (fig. 390, *cr*). The cavity of the canal of the cochlea is thus rendered continuous with that of the saccule. The structures which are found upon the *floor* of this spirally-wound triangular canal of the cochlea claim more particular attention, for it is to them that the branches of the cochlear nerve are distributed, and upon them the function of the cochlea as a part of the auditory apparatus appears more especially dependent.

The floor itself of the cochlear canal is formed of a narrow portion of the spiral lamina external to the membrane of Reissner, and of the basilar membrane. In the macerated specimen this part of the lamina thins off gradually to a fine edge like the blade of a knife, but in the recent condition (fig. 398, *lls*) it retains its thickness for some distance (or even exhibits a slight increase), and then abruptly terminates with a border which in section is C-shaped, with the lower limb of the C much more prolonged and tapering than the upper. The lower limb is in fact the section of the end of the osseous lamina, together with a thin membranous layer which covers it, and which is directly prolonged into the basilar membrane. This membrane, as well as the whole thickened upper part of the edge of the spiral lamina, not being ossified, disappears in the process of maceration. The thickened part (fig. 398, *lls*), with its somewhat overhanging, crest-like end (fig. 400, *Cr*), is known as the *limbus* of the spiral lamina, and the groove which it overhangs, and which in section is represented by the bay of the C, is known as the *spiral groove* (fig. 398, *ss*, fig. 400, *S. sp. i*).

The tissue of which the **limbus** is composed seems to be a form of connective tissue. Towards the under and inner part there are numerous corpuscles, and the texture is fibrous, but above and near the crest few or no connective tissue corpuscles are met with, but the tissue has a columnar aspect with somewhat regularly arranged nuclei. The fibrillated tissue is prolonged, as just intimated, beyond the osseous lamina, into the basilar membrane. Near its termination, close to the junction with the basilar membrane, it is perforated with a number of regularly-arranged, elongated apertures (fig. 399, *p*), which serve for the transmission upwards of the nerve-fibres. The latter, in their course from the spiral ganglion to the auditory epithelium, are lodged, as far as this, in canals

in the lower osseous part of the spiral lamina. Their arrangement will be afterwards more fully described.

When the limbus is viewed from above, the edge is seen to present a succession of tooth-like projections (fig. 399, *Cr*), which give it a jagged aspect. These projections are continued as flattened eminences a short distance on the upper surface of the limbus, which is, therefore, not smooth, at least near the edge, but marked in this way with eminences and intervening furrows. Nearer the line of origin of the membrane of Reissner, it becomes smoother, and here, too, its epithelial covering, which is directly continuous with that of the under surface of Reissner's membrane, is evenly distributed; whereas at the crest itself the epithelial cells are, in the adult, only found in the furrows: so that the tooth-like prominences project between the rows of epithelium into the cochlear canal. Immediately below the overhanging projections, the epithelium again forms a layer which lines the spiral groove, and is continuous externally with the specialized cells, presently to be described as forming the organ of Corti.

The **basilar membrane** stretches, as before mentioned, straight between the osseous lamina and the spiral ligament, and separates the canal of the cochlea from the scala tympani. It increases in breadth, at first rapidly but afterwards more gradually, from the base to the apex of the cochlea, while the breadth of the osseous spiral lamina diminishes. Thus in the first turn of the cochlea, this membrane forms about half of the breadth of the septum, meaning about 0.041 mm.; but

Fig. 399.

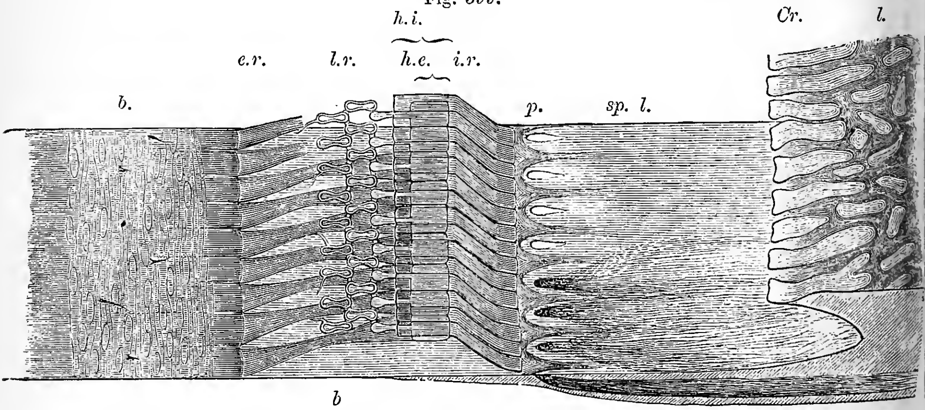


Fig. 399.—Semi-diagrammatic view of part of the basilar membrane and tunnel of Corti of the rabbit, from above and the side. Much magnified. (E.A.S.)

l, limbus; *Cr*, extremity or crest of limbus with tooth-like projections; *b b*, basilar membrane; *sp.l*, spiral lamina with, *p*, perforations for transmission of nerve-fibres. In the lower half of the part of the spiral lamina here represented the nerve fibres are left, and are supposed to be seen through the upper layer of that lamina, converging to three of the perforations; below, in the section of the lamina, they are shown occupying a canal, or cleft, in the osseous substance; *i.r*, fifteen of the inner rods of Corti; *h.i*, their flattened heads seen from above; *e.r*, nine outer rods of Corti; *h.e*, their heads, with the phalangeal processes extending outward from them and forming, with the two rows of phalanges, the lamina reticularis, *l.r*. On the left of the figure the connective tissue fibres and nuclei of the undermost layer of the basilar membrane are seen through the upper layers. Portions of the basilar processes of the outer hair-cells remain attached here and there to the membrane at this part.

towards the apex of the cochlea, the proportion between the two parts is changed, until, near the helicotrema, the membranous part is left almost unsupported by any plate of bone, measuring as much as 0·495 mm., or about twelve times as much as at the base (Hensen). The exact nature of the tissue composing the proper substance of the membrane is unknown, but it is probably analogous to that composing the rods of Corti, to be afterwards described. It is somewhat stiff in consistence, and may readily be broken up into straight fibres which have a radial direction, corresponding with a striation which the membrane, especially its outer part, presents when viewed on the surface (fig. 399). Externally at its attachment to the spiral ligament, it breaks up into diverging fibres, which spread into that projection. On the upper surface of the membrane is the epithelium which forms the organ of Corti, and the single layer of cells which is continued from this externally (fig. 400): on the under surface it is covered by a layer of connective tissue (often described as part of the membrane), the fibres of which have a direction parallel with the spiral, and across that of the fibres of the membrane proper. There are numerous intermixed spindle-shaped corpuscles in this tissue, which is in continuity with the lining periosteum of the scala tympani (fig. 399). Small blood-vessels are found in it, but as a rule extending only over the inner part of the membrane. They are usually terminated by a rather larger longitudinally running vessel, situated opposite the outer rods of Corti, and known as the *vas spirale.*

The **membrane of Reissner** (figs. 398, 400, *R*), separates the scala vestibuli from the canal of the cochlea. It is composed of an exceedingly delicate layer of connective tissue continuous with the lining periosteum of the scala vestibuli, and is covered on the surface which is turned to the cochlear canal with a simple pavement epithelium which is in continuity below with the epithelium of the limbus and above with that lining the outer wall of the canal (fig. 400). The cells have each a circular flattened nucleus, and not unfrequently contain fat droplets. The vestibular side of the membrane of Reissner is quite smooth, and is covered with an epithelioid layer of flattened connective-tissue cells, distinguishable from the epithelial cells on the other side by their greater delicacy of outline, and their larger size. A few blood-capillaries are continued into the membrane from the neighbouring periosteum.

Outer wall of the cochlear canal.—The periosteum which lines the scala vestibuli and scala tympani, consists of ordinary connective tissue. There is no continuous lining of flattened cells on the free surface, such as covers the surface of serous membranes. On the other hand the periosteum which bounds the canal of the cochlea externally, is much thickened by a development of retiform connective tissue, and is covered by the epithelium of that tube, which here forms a single layer of cubical or columnar cells, many of which contain pigment. There is usually a slight inward projection a little above the spiral ligament, containing a prominent blood-vessel (fig. 400, *L. sp. a*). In the tract between this prominence and the membrane of Reissner, the substance of the periosteum is also frequently pigmented, and from containing large and numerous blood-vessels, the capillary loops of which may even project between the bases of the epithelium-cells, is termed *stria vascularis* (*St. v.*). Immediately beneath the epithelium of the outer wall is a basement membrane, through which, in section, cell-

processes may here and there be seen passing into the epithelium from the subjacent connective tissue.

The **spiral ligament** (fig. 400, *Lsp*) appears in section as a triangular prominence attached to the outer wall of the cochlea, with the basilar membrane prolonged from its apex. It is composed of a retiform connective tissue, many of the cells of which have an elongated shape and radiate from the point of attachment of the basilar membrane. They have been considered by some to be muscular, but there is no distinct proof of their contractile nature.

Fig. 400.

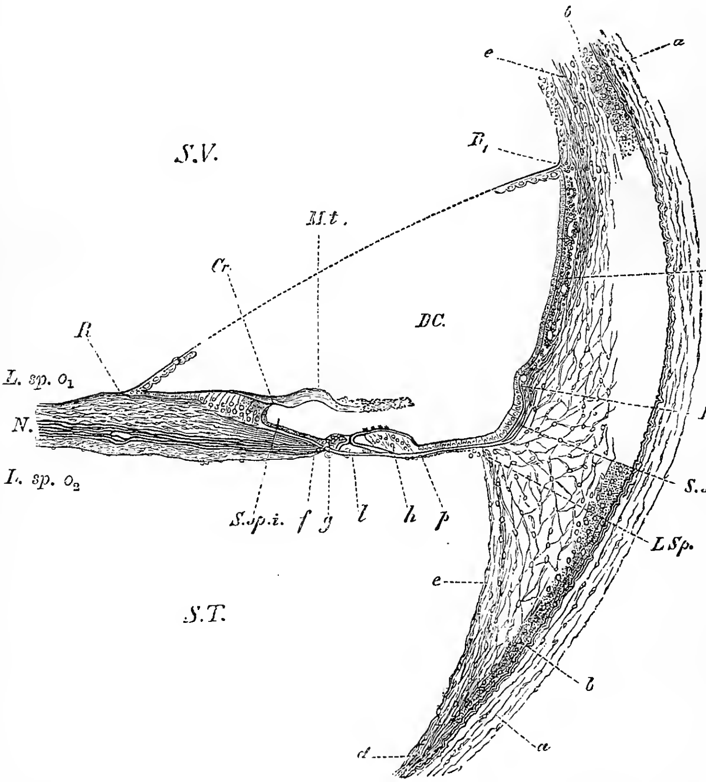


Fig. 400.—Vertical section of the first turn of the cochlea of a child a year and a half old. 100 diameters (Waldeyer).

SV, scala vestibuli; *ST*, scala tympani; *DC*, duct or canal of the cochlea; *L.sp.o*$_1$, *L.sp.o*$_2$, vestibular and tympanal layer of the osseous spiral lamina with the stratum of nerve-fibres, *N*, between; *a*, *a*, outer bony wall of the cochlea; *b*, *b*, and *d*, periosteum; *e*, *e*, connective tissue thickening forming at *L.Sp.* the spiral ligament; *St.v.*, stria vascularis; *L.Sp.a*, prominence known as the *accessory spiral ligament*, containing a spirally running blood-vessel, the *vas prominens;* *S.sp.i.*, spiral groove (inner); *S.sp.e.*, so-called *external spiral groove;* *R*, *R*$_1$, section of Reissner's membrane, the middle part indicated only by a dotted line; from *R* to *Cr.*, limbus laminæ spiralis; *M.t.*, membrana tectoria, somewhat raised up from its natural position; *f—p*, organ of Corti; *f*, nerves turning up to enter epithelium; *g*, inner hair-cell region; *h*, region of the outer hair-cells; *l*, basilar membrane underneath rods of Corti.

Organ of Corti.—The epithelium which covers the basilar membrane requires a careful description, including as it does the highly-specialised structures which are known by the name of the **organ of Corti.** The central part of this apparatus is formed by two sets of stiff, rod-like bodies—the inner and outer *rods of Corti* (figs. 401, 402)—

Fig. 401.

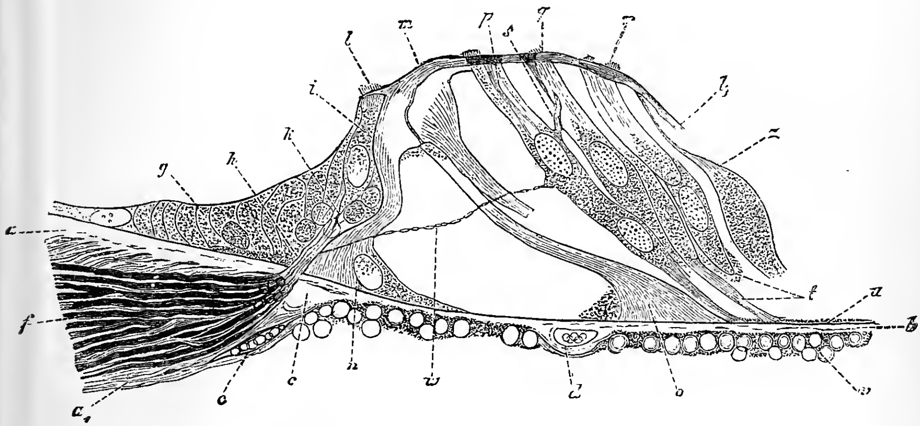


Fig. 401.—Section of the organ of corti of the dog (from Waldeyer). $\frac{800}{1}$.

a, *a'*, end of spiral lamina ; *b*, *c*, middle (homogeneous) layer of the basilar membrane ; *u*, vestibular (striated) layer ; *v*, tympanal (connective tissue) layer ; *d*, blood-vessel ; *f*, nerves in spiral lamina ; *g*, epithelium of spiral groove ; *h*, nerve-fibres passing towards inner hair-cells, *i*, *k* ; *l*, auditory hairlets on inner hair-cells ; *l*, *l'*, lamina reticularis ; *m*, heads of the rods of Corti, jointed together ; the inner rod is seen in its whole length ; the outer one is broken off half way, and the next one comes into view ; *n*, cell at base of inner rod ; *p*, *q*, *r*, outer hair-cells ; *s*, a cuticular process extending upwards, and probably belonging to a cell of Deiters ; *t*, lower ends of hair cells ; two of them are attached by cuticular processes to the basilar membrane ; *w*, a nerve-fibril passing into an outer hair-cell ; *z*, a sustentacular cell of Deiters.

which stand upon the basilar membrane, the outer series (*e.r.*), at some little distance from the inner (*i.r.*), and are inclined towards each other, coming in contact above. In this way each pair of rods forms a pointed arch with slanting sides (fig. 402), and since the rods of each series are

Fig. 402.

Fig. 402.—A pair of rods of corti, from the rabbit's cochlea, in side view. (E.A.S.) Highly magnified.

b, *b*, basilar membrane ; *i.r*, inner rod ; *e.r*, outer rod. The nucleated protoplasmic masses at the feet are also shown.

in lateral juxtaposition, the double row of inclined columns forms a tunnel (fig. 399) along the whole extent of the cochlear canal.

On the inner side of the inner series of rods is a row of epithelial cells (fig. 401, *i*), which are surmounted by a brush of fine, short, stiff hairlets, and external to the outer rods are three or four successive rows of similar

but more elongated cells (p, q, r). These cells are termed respectively the *inner* and *outer hair-cells*. The hairlets of the outer hair-cells project through apertures in a curiously formed cuticular membrane, termed the *reticular lamina* (399, *l. r.*), which covers this part of the organ of Corti like a wire net. On either side of the two sets of hair-cells the epithelium, becoming gradually shorter, passes continuously into the simple layer of cubical cells which is found in the spiral groove and on the lateral part of the basilar membrane.

The whole organ is further covered by a thick, fibrillated membrane —the *tectorial membrane* (fig. 400, *M.t.*)—which is attached at one edge to the upper surface of the limbus, falls over the crest, and rests on the rods of Corti and the hair-cells, thus converting the spiral groove into a canal. It will be necessary to describe more minutely these several parts of the organ of Corti.

Rods of Corti.—The inner and outer rods of Corti differ from one another in shape, although agreeing, for the most part, as regards the details of their structure. Each inner rod may be best compared in shape to a human ulna, the upper end of the rod being pretty accurately

Fig. 403.

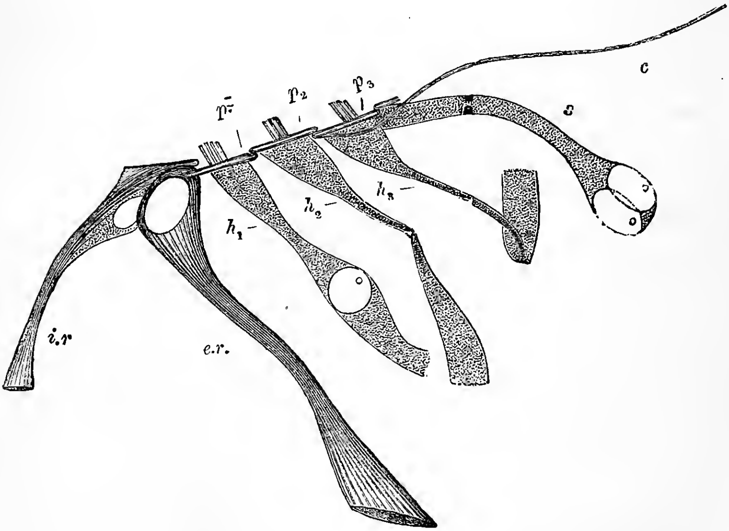


Fig. 403.—Profile view of an inner and an outer rod in connection with three hair-cells, and part of the lamina reticularis (from the guinea-pig). (E.A.S.) Very highly magnified.

i.r, inner rod; *e.r*, outer rod; h_1, h_2, h_3, hair-cells of first, second, and third rows respectively. They appear, especially the second and third, narrow in the middle, the thin edge of the riband-shaped cell being here seen, but below have become accidentally twisted so that the flattened side is brought into view. A nucleus is visible in h_1, but none is seen in h_2, h_3, probably owing to its being contained in the part of the cell the edge of which is turned towards the observer. The lower ends of all three, together with their basilar processes, have become broken off in the preparation of the specimen; *s*, one of the succeeding epithelial cells; *c*, cuticular thread attached to lamina reticularis, and probably belonging to a cell of Deiters; *p*, phalangeal process of outer rod; p_2, p_3, phalanges of lamina reticularis seen in section.

represented by the upper extremity of that bone, the shape of the olecranon and coronoid processes, as well as the concave articular surface between, being readily recognisable. The upper end of one of the outer rods, on the other hand, somewhat resembles the outline of a swan's head ; the rounded part, which represents the back of the head, fitting into the concave surface on the head of the corresponding inner rod or rods, while the part which represents the bill projects outwards and is connected with the reticular lamina, aiding to form the first series of rings for the transmission of the auditory hairlets. Both inner and outer rods are more slender about the middle of their length and expand again below, so as to rest upon the basilar membrane by a somewhat widened foot. They are distinctly striated throughout their length (fig. 403), and the striation or fibrillation passes into that of the basilar membrane, to which they are thus intimately connected (fig. 399). This is especially well seen in the outer rods.

In the head of the outer rod is an oval part free from fibres, and staining with carmine more deeply than the remainder of the rod : this may represent the nucleus of an epithelial cell from which the rod was originally developed. A similar, but smaller clear body, staining deeply with carmine, is sometimes to be seen in the head of the inner rod, and the substance of the rod in its neighbourhood has a somewhat granular appearance (fig. 403).

In connection with both inner and outer rods, there is seen a protoplasmic cell occupying the angle which the rod makes with the plane of the basilar membrane (fig. 402). Sometimes these cells extend along the membrane until they come into contact.

The inner rods are more numerous than the outer ;* they are also more closely set and touch one another along their whole length, whereas the outer rods are only in contact laterally by their heads ; finally the outer rods are in all parts longer than the inner, and in the upper turns of the cochlea considerably so.

How the two sets of rods are jointed together is not very clear. It is certain that the individual rods have little, if any, independent movement ; they are securely fixed below to the basilar membrane, and the heads of adjacent rods are in close contact.

Hair-cells.—The *inner hair-cells* are closely applied against two or three of the corresponding rods, the cells being considerably larger in diameter than the rods. They are very like somewhat short, columnar epithelium-cells, and are prolonged below into a process, or it may be more than one, which, according to Waldeyer, is directly connected to one of the nerve fibres which turn up through the spiral lamina just below these cells (fig. 401). Beneath them, and extending also under the gradually decreasing columnar epithelium of the spiral groove, is a layer of protoplasmic cells with large round nuclei, amongst which fine nerve-fibres are said to run in a radial direction. Around the top of each inner hair-cell is a sort of ring of cuticular substance, which is connected with slight projections on the flattened heads of the inner rods, and appears to represent the reticular lamina in this place.

The *outer hair-cells* are peculiar in shape. They are cylindrical at the upper end, where they fit into the rings of the reticular lamina and

* According to Waldeyer there are altogether in the human cochlea about 6000 of the inner rods and 4500 of the outer ones.

bear the hairlets, but lower down they are flattened from within out, so that, in profile, they look narrow, but broader when seen on the flat (fig. 403). These cells end below with a rounded extremity (fig. 404, *b*) slightly bulged to one side, whilst from the other side a thin cuticular

Fig. 404.

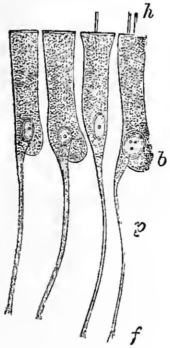


Fig. 404.—FOUR OUTER HAIR-CELLS IN CONNECTION WITH THEIR BASILAR PROCESSES. FROM THE GUINEA-PIG. HIGHLY MAGNIFIED. (E.A.S.)

The cells belong to the same series and are viewed flat. *h*, one or two hairlets which have remained attached; *b*, bulged lower end of cell; *p*, basilar process, protoplasmic above but becoming cuticular below and slightly expanded at the extremity *f*, which is broken away from the basilar membrane.

process (*p*) is prolonged which is fixed to the basilar membrane (basilar process). Beneath the hair-cells and resting by a broad base upon the basilar membrane, certain other cells are found which are known as the *cells of Deiters* (fig. 401, *z*). These extend upwards for a certain distance between the lower ends of the hair-cells, and each one is then prolonged towards the surface by a fine cuticular process, which is attached above to one of the so-called phalanges of the reticular lamina, and is known as the phalangeal process.

Hensen describes a clear oval capsule with a spiral fibre wound around it, occupying the part of the cell next to the free extremity.

According to Waldeyer the outer hair-cells and the cells of Deiters are, in the dog and some other animals, conjoined to form double cells with two nuclei.

Fig. 405.

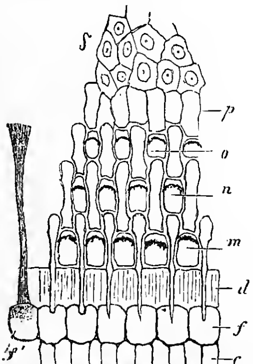


Fig. 405.—SKETCH FROM BELOW OF LAMINA RETICULARIS AND ADJOINING STRUCTURES FROM THE CAT. HIGHLY MAGNIFIED (Kölliker).

a, inner hair-cells with hairlets, *β*; *e*, epithelium of spiral groove; *c*, inner rods; *d*, part of heads of inner rods overlapping those of the outer rods; *f*, heads of outer rods: their long phalangeal processes are seen, but the rods themselves are not represented, except at *f′*; *m*, *n*, *o*, rings of lamina reticularis with semicircles of hairlets, the hair-cells not being represented; *p*, cuticular tissue between external epithelial cells, *δ*.

In most animals there are three series of outer hair-cells, but in man there are four series (fig. 400, *h*) and even five and six in the upper turns of the cochlea (Pritchard). The columnar cells outside the hair-cells are much elongated and obliquely disposed, but become gradually shorter and more vertical as they pass into the simple cubical epithelium on the outer part of the basilar membrane.

Lamina reticularis (figs. 399, 405).—The net-like membrane which overlies the outer hair-cell region of the organ of Corti is composed of at least two rows of elongated fiddle-shaped structures termed "phalanges" which are united to one another and to the phalangeal processes of the outer rods in such a manner as to leave between them oblong apertures

through which the free ends of the hair-cells with their semicircular rows of auditory hairs project. The phalanges, although they seem like rings, are in reality thin plates with thickened margins, and are to all appearance of a cuticular nature: the most external row of phalanges is in continuity with a cuticular tissue which lies between the external epithelium cells (fig. 405, *p*). Attached to the phalanges below are the phalangeal processes of the cells of Deiters. The lamina varies in extent with the number of rows of hair-cells. Where there are four or more of these, a corresponding increase in the number of rows of phalanges is observed. The phalanges serve to isolate the hair-bearing ends of the auditory cells.

The **tectorial membrane** is the last special structure which remains to be described in connection with the organ of Corti. It arises, as before stated, on the limbus, not far from the line of origin of Reissner's membrane. It overlies the projecting teeth at the edge of the limbus, and also the epithelium between them: all this part of the membrane is thin and delicate, imperceptibly shading off towards the inner edge of attachment. As the membrane projects over the crest of the limbus, it swells out below into a pad-like projection which covers in and partly fills up the spiral groove, and rests below upon the rods of Corti and contiguous structures. Towards its external edge the membrane again thins out, and over-lies the outer hair-cell region as a delicate film presenting a somewhat reticular appearance, as if impressed by or moulded on the subjacent structures. The thickened part of the membrane is distinctly fibrous in appearance (the fibrillation extending from within out), and after immersion in weak solutions of chromic acid, or bichromate of potash, it appears to possess considerable toughness and elasticity. From its position the hairlets borne by the hair-cells must necessarily be in contact with the under surface of this membrane. About its origin nothing certain is known, but it appears to be formed as a cuticular deposit or secretion from the epithelial cells, upon which, even at a comparatively early stage of development, it may be seen to lie. In the position which it bears relative to the auditory epithelium it corresponds to the cupulæ terminales of the cristæ acusticæ and to the otolithic accumulations of the maculæ.

Nerves of the cochlea.—The branch of the auditory nerve which goes to the cochlea is given off in common with those to the saccule and the posterior ampulla. It is shorter, flatter, and broader than any of the other branches. It perforates the bone by groups of minute foramina at the bottom of the internal meatus, below the opening of the Fallopian aqueduct. These groups are arranged in a shallow spiral furrow (tractus spiralis foraminulentus) in the centre of the base of the cochlea; and they lead into small bony canals, which first follow the direction of the axis of the cochlea, through the modiolus, and then radiate outwards, between the plates of the bony spiral lamina. In the centre of the spiral tract is a larger foramen which leads to the central canal of the modiolus. Through this foramen and canal the filaments for the last half-turn of the spiral lamina are conducted; whilst the first two turns are supplied by the filaments which occupy the smaller foramina and bent canals. Near the root of the spiral lamina the nerve-fibres pass outwards through a spirally wound ganglionic cord, (*ganglion spirale*) situated in the special bony canal (*spiral canal of the modiolus*) already mentioned. The cells of this ganglion are bipolar and each nerve-fibre appears to have one of the cells interpolated in its course. From the outer

side of the ganglion, the fibres, having resumed their medullary sheath, pass onwards with a plexiform arrangement, at first in distinct but anasto-

Fig. 406.

Fig. 406. — General view of the mode of distribution of the cochlear nerve, all the other parts having been removed.

mosing cords (fig. 407, B, 3), contained in separate canals in the bony lamina, but afterwards spreading out into a stratum of intermingling fibres, to be again gathered up, near the edge of the osseous lamina, into

Fig. 407.

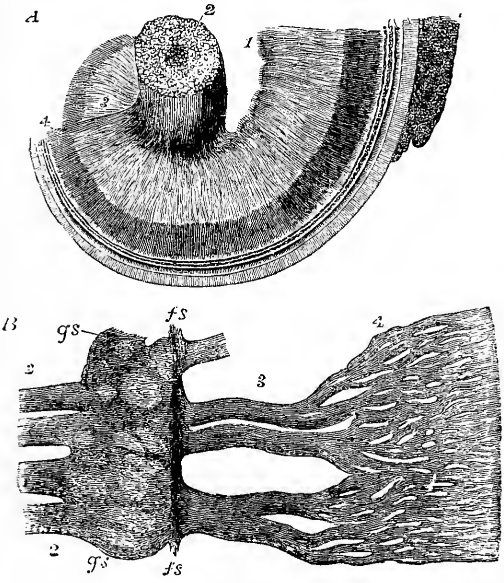


Fig. 407.—Distribution of the cochlear nerves in the spiral lamina (after Henle).

A, part of the modiolus and spiral lamina, viewed from the base, showing the plexiform arrangement of the cochlear nerves ; 1, filaments of the nerve issuing from the tractus spiralis foraminulentus ; 2, branches of the nerve entering the central canal of the modiolus ; 3, wide plexus in the bony lamina spiralis ; 4, close plexus at its border. *B*, part of the nerves extracted and more highly magnified ; 2, twigs of the nerve from the modiolus close to the lamina spiralis ossea ; *gs*, spiral ganglion ; *fs*, nerve-fibres running spirally along the outer part of the ganglionic swelling ; 3, wide plexus ; 4, close plexus of nerve-fibres as in *A*.

conical bundles which turn abruptly upwards, and passing through the elongated apertures previously described (p. 457 and fig. 399, *p*), enter the epithelium in the region of the inner hair-cells (fig. 401, *h*).

Little is known positively with regard to the actual mode of ending of the nerves amongst these structures. As they pass through the apertures in the

membrane, they lose their medullary sheath and dark borders, and are continued as simple axis-cylinders. Their further course is still a matter of doubt. Some of them are stated by Waldeyer to pass directly into the lower ends of the inner hair-cells, and others to pass outwards between the rods of Corti, stretching across the tunnel which these enclose, and eventually ending in the outer hair-cells; but these statements, although not improbable, yet require confirmation.

Vessels of the cochlea.—The branches of the internal auditory artery to the cochlea, twelve or fourteen in number, arising at the bottom of the internal auditory meatus, traverse small canals in the modiolus and bony lamina spiralis, and form in the latter a capillary plexus that joins at intervals the vas spirale, previously mentioned. From this plexus offsets are distributed in the form of a fine network on the periosteum, but the vessels do not anastomose across the membrana basilaris. The cochlea also receives through the fenestra rotunda a twig from the stylomastoid branch of the occipital artery.

The veins of the cochlea issue from the grooves of the cochlear axis, and join the veins of the vestibule and semicircular canals at the base of the modiolus. A small sinus-like vein passes through the aqueductus cochleæ, from the lowermost turn of the cochlear tube, and joins the commencement of the internal jugular vein.

Measurements of some of the parts of the cochlea.—The following numbers show the average dimensions of various parts of the human cochlea. They are copied from Waldeyer (article "Cochlea" in Stricker's Handbook), and represent the size in micromillimeters.*

Cochlear canal, breadth, 1st turn	800 μ
" " " 2nd turn	700
" " , extreme height	500
Reissner's membrane, breadth, 1st turn	900
" " " 2nd turn	700
Limbus laminæ spiralis, breadth, 1st turn	300
" " " " 2nd turn	200—250
Rods of Corti, space between attachment of feet	66—70
" " height of arch	12
" " length of inner rods	50
" " length of outer rods	60—66
Hair-cells, length of inner	18
" " length of outer, with basilar process	48
" " length of hairlets	4
Membrana tectoria, extreme breadth	200—230
" " extreme thickness	50

Recent Literature of the Ear.—On the external ear:—*Kessel*, in Stricker's Handbook, 1872; *v. Troeltsch*, Handb. d. Ohrenheilk., 1881.

On the tympanic cavity and ossicles:—*Kessel*, in Stricker's Handbook, 1872, and Arch. f. Ohrenheilk., 1874 (action of muscles); *Rüdinger*, in Monatschr. f. Ohrenheilk., 1872; and "Beiträge &c.," 1873; *Weber* in Monatschr. f. Ohrenh., 1872 (tensor tympani); *Brunner*, in Knapp u. Moos' Arch., 1873 (articulations of ossicles); *Urbantschitsch*, in Arch. f. Ohrenheilk., 1873 and 1876; *Politzer*, in same journal, 1875 and 1876 (muscles, and vessels); *Moldenhauer*, in same journal, 1876, and Vergleichende Histol. d. Trommelfells, Arch. f. Ohrenheilk., 1878; *Moos*, in Knapp u. Moos' Arch., 1877 (vessels of membrane); *Körner*, in Monatschr. f. Ohrenheilk., 1878; *Hensen*, Article "Gehör," in Hermann's Handb., 1880.

On the Eustachian tube:—*Mach u. Kessel*, in Wiener Sitzungsb., 1872; *Weber-Liel*, "Ueber das Wesen, &c.," Berlin, 1878; *Moos*, Wiesbaden, 1874; *Zuckerkandl*, in Monatschr. f. Ohrenheilk., 1874; *Yule*, in Journ. of Anat. and Physiol., 1874; *Urbanschitsch*, in Arch. f. Ohrenheilk., 1875; and Wiener med. Jahrb., 1875; *Zaufal; Michel*, in Arch. f. Ohrenheilk., 1875 and 1876; *Lucæ*, in Virch. Arch., 1875 and 1878; *Gerlach*, in Erlangen Sitzungsb., 1875.

On the membranous labyrinth:—*Rüdinger*, in Stricker's Handb., 1872; *G. Retzius*, Anat. Unters. 1872; "Morphologie des Gehörlabyrinths," Stockholm, 1881; and "Biologische Studien," 1882; *v. Ebner*, Epith. d. crista acust., Schriften d. med. Ver

* A micromillimeter is the $\frac{1}{1000}$th part of a millimeter, or the $\frac{1}{25000}$th part of an inch, and is generally represented by the Greek letter μ.

zu Innsbrück, 1872; *Hasse*, Anat. Studien, 1872; and Vergleichende Morphol. &c., 1873; *Urban Pritchard*, Nerves of Vest. and Semic. Canals, Quarterly Journal of Micr. Science, 1876; *P. Meyer*, Étude histologique, &c., 1876; *Weber-Liel* in Med. Centralbl., 1876, and Monatschr. f. Ohrenh., 1876 (fenestra rotunda).

On the aqueductus vestibuli and saccus endolymphaticus:—*Key and Retzius*, in Studien ü. d. Nervensystem, &c., 1874; *Zuckerkandl*, in Monatschr. f. Ohrenheilk., 1876; *Weber-Liel*, in Centralbl. f. d. med. Wissensch., 1876, and Monatschr. f. Ohrenheilk., 1879; *Rüdinger*, in Zeitschr. f. Anat. u. Entw., 1876.

On the cochlea:—*Waldeyer*, in Stricker's Handb., 1872; *Gottstein*, in Arch. f. mikr. Anat., 1872; *Urban Pritchard*, in Proc. Roy. Soc., 1872, and 1876; *Böttcher*, in Dorpat med. Zeitschr., 1873; *Hensen*, in Arch. f. Ohrenheilk., 1873 and 1874; *Lavdovsky*, in Arch. f. mikr. Anat., XIII.; *Nuel*, Mem. cour., Bruxelles, 1878.

THE NOSE.

The nose is the special organ of the sense of smell. It has also other functions to fulfil;—for, communicating freely with the cavities of the mouth and lungs, it is concerned in respiration, voice, and taste; and by means of its muscles it assists in expression.

Fig. 408.

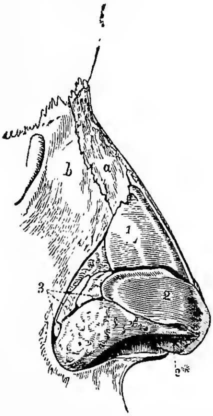


Fig. 409.

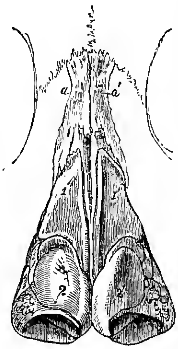


Fig. 410.

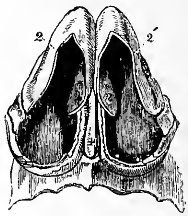


Fig. 408.—Lateral view of the cartilages of the nose (Arnold). $\frac{3}{4}$

a, right nasal bone; *b*, nasal process of the superior maxillary bone; 1, upper lateral cartilage; 2, lower lateral cartilage; 2*, inner part of the same; 3, sesamoid cartilages, here distinct, but generally united with the lower lateral cartilage.

Fig. 409.—Front view of the cartilages of the nose (Arnold). $\frac{3}{4}$

a, *a'*, nasal bones; 1, 1', upper lateral cartilages; 2, 2', lower lateral cartilages.

Fig. 410.—View of the cartilages of the nose from below (Arnold). $\frac{3}{4}$

2, 2', outer part of the lower lateral cartilages; 2*, 2*, inner part of the same; 4, lower edge of the cartilage of the septum.

The nose consists of the anterior prominent part, composed of bone and cartilages, with muscles (already described in Vol. I.), and with two orifices, *anterior nares*, opening downwards; and of the two nasal fossæ, in the upper parts of which the olfactory nerves are expanded. The nasal fossæ are separated from each other by a partition, *septum nasi*, formed of bone and cartilage in the greater part of its extent, but prolonged between the anterior nares only by a thick fold of integument termed the membranous septum or *columna nasi*. The nasal fossæ communicate with hollows in the neighbouring bones (ethmoid, sphenoid, frontal, and superior maxillary); and they open backwards into the

pharynx through the *posterior nares*. The skin of the nose is studded, particularly in the grooves of the alæ or outer walls of the nostrils, with numerous small openings, which lead to sebaceous follicles. Within the margin of the nostrils there is a number of short, stiff, and slightly curved hairs—*vibrissæ*—which grow from the inner surface of the alæ and septum nasi.

CARTILAGES OF THE NOSE.

These are the chief support of the outer part of the organ. They occupy the triangular interval seen in front of the nasal cavity in the dried skull (anterior nasal aperture), and assist in forming the septum between the nasal fossæ. There are two large cartilages on each side, and one mesial cartilage of the septum.

The *upper lateral cartilages* (figs. 408 and 409, 1) are situated in the upper part of the projecting portion of the nose, immediately below the free margin of the nasal bones. Each is flattened and triangular in shape, and presents one surface outwards, and the other inwards towards the nasal cavity. The anterior margin, thicker than the posterior, meets the lateral cartilage of the opposite side above, but is united with the edge of the cartilage of the septum below; indeed, by some anatomists, as Henle, the upper lateral are described with the median cartilage, of which they may be regarded as reflected wings. The inferior margin is connected by fibrous membrane with the lower lateral cartilage; and the posterior edge is closely attached to the free margins of the upper maxilla and of the nasal bone.

The *lower lateral cartilages* (cartilages of the aperture) (2, 2′, in the figures) are thinner than the preceding, below which they are placed, and are chiefly characterised by their peculiar curved form. Each consists of

Fig. 411.

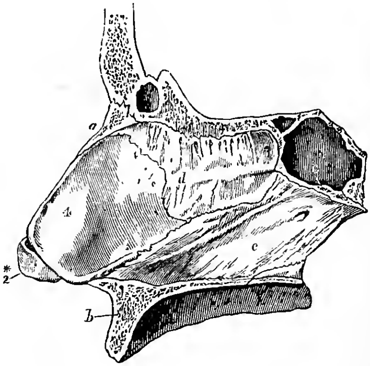


Fig. 411.—Osseous and cartilaginous septum of the nose, seen from the left side (Arnold). $\frac{2}{3}$

a, right nasal bone; *b*, superior maxillary bone; *c*, sphenoidal sinus; *d*, perpendicular plate of the ethmoid bone; *e*, vomer; 2*, inner part of the right lower lateral cartilage; 4, cartilage of the septum.

an elongated plate, so bent upon itself as to pass in front and on each side of the nostril to which it belongs, and by this arrangement serve to keep it open. The outer portion is somewhat oval and flattened, or irregularly convex externally. Behind, it is attached to the margin of the upper maxilla by tough fibrous membrane, enclosed in which there is usually to be met with either a prolongation backwards of the posterior angle of the cartilage, or two or three separate cartilaginous nodules (*cartilag. minores vel sesamoideæ*) (fig. 408, 3); above, it is fixed, also by fibrous membrane, to the upper lateral cartilage, and to the lower and fore part of the cartilage of the septum. Towards the middle line it is curved backwards (fig. 409), bounding a deep

mesial grove, at the bottom of which it meets with its fellow of the opposite side, and continues to pass backwards, lying in the upper part of the columna nasi, below the level of the cartilage of the septum. This inner part of the cartilage of the ala is thick and narrow, curls outwards, and ends in a free rounded margin (fig. 411, 2*), which projects outwards. The greater part of the ala of the nose, like the lobule of the ear, is formed of thickened skin with subjacent tissue, and is unsupported by cartilage.

The *cartilage of the septum* (fig. 411, 4) is quadrilateral in form, and is thicker at the edges than near the centre. It is placed nearly vertically in the middle line of the nose, and completes, at the fore part, the separation between the nasal fossæ. The anterior margin of the cartilage, thickest above, is firmly attached to the back of the nasal bones near their line of junction; and below this it lies successively between the upper and the lower lateral cartilages, united ultimately with the former and loosely with the latter. The posterior margin is fixed to the lower and fore part of the central plate of the ethmoid bone (*e*); and the lower margin is received into the groove of the vomer (*v*), as well as into the median ridge between the superior maxillæ.

This cartilage is the persistent anterior extremity of the primordial cranium. In young subjects it is prolonged back to the body of the pre-sphenoid bone; and in many adults an irregular thin band remains between the vomer and the central plate of the ethmoid.

NASAL FOSSÆ.

The nasal fossæ, and the various openings into them, with the posterior nares, have been previously described as they exist in the skeleton,

Fig. 412.

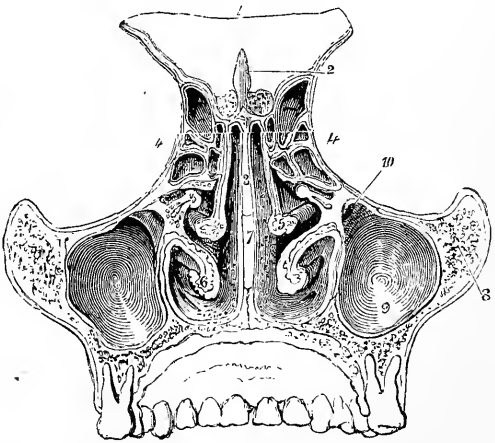


Fig. 412.—Transverse vertical section of the nasal fossæ seen from behind. (Arnold). $\frac{3}{4}$

1, part of the frontal bone; 2, crista galli; 3, perpendicular plate of the ethmoid; between 4 and 4, the ethmoidal cells; 5, right middle spongy bone; 6, left lower spongy bone; 7, vomer; 8, malar bone; 9, maxillary sinus; 10, its opening into the middle meatus.

and the greater part of that description is also applicable generally to the nose in a recent state; but there are certain differences which depend on the thickness of the lining membrane, which not only lines the walls of the fossæ, but covers the spongy bones on both sides. Thus, in the first place, the nasal cavity is much narrower in the recent state. Secondly, in consequence of the prolongations of the membrane on their free margins, the turbinate bones, and more particularly the lower pair, appear to be both more prominent, and longer, than in the dried skull. Thirdly, some of the foramina in the bones are narrowed, and others covered over by the lining membrane.

In the individual parts of the nasal fossæ the following particulars are to be noticed.

In the *upper meatus*, the small orifice which leads into the posterior ethmoidal cells is lined by a prolongation of the thin mucous membrane which is continued into those cavities; but the spheno-palatine foramen is covered over and closed by the membrane.

In the *middle meatus*, the aperture of the infundibulum is nearly hidden by an overhanging fold of membrane: it leads directly into the anterior ethmoidal cells, and through them into the frontal sinus. Below and behind this, the passage into the antrum of Highmore is surrounded by a fold of the membrane (sometimes prominent and even slightly valvular), which leaves a circular aperture much smaller than the foramen in the bony meatus.

In the *lower meatus* the inferior orifice of the nasal duct is defended by one or two folds of membrane; and when there are two, the folds are often adapted so accurately together as to prevent air from passing back from the cavity of the nose to the lachrymal sac.

In the *roof* the apertures in the cribriform plate of the ethmoid bone are concealed by the membrane, but the openings into the sphenoidal sinuses receive a prolongation from it.

In the *floor* the incisor foramen is in the recent state generally closed. Sometimes, however, a narrow funnel-shaped tube of mucous membrane (naso-palatine canal or canal of Stenson) passes obliquely downwards from each nasal fossa for a short distance towards the front of the hard palate. Vesalius, Stenson, and Santorini believed that these tubes of membrane opened generally into the roof of the mouth by small apertures close behind the central incisor teeth. Haller, Scarpa, and Jacobson, found the canals in man usually closed, and often difficult of detection.

Modern anatomists have also been divided in opinion on this matter, but it would appear that the latter opinion (that of Haller and Scarpa) is correct. The canal is the remnant of the wide communication between the nasal and buccal cavities found at an early period of fœtal life, being in man usually obliterated, at least in its lower part, before birth, although persistent in many animals. It is long represented below by a solid column of epithelium cells continuous with the epithelium of the palate, and above by a narrow tube lined with ciliated epithelium, opening into the floor of the nasal fossa but closed below. (Leboucq, Le canal nasopalatin chez l'homme, Archives de Biologie, 1881.)

MUCOUS MEMBRANE.

The pituitary or Schneiderian membrane, which lines the cavities of the nose, is a highly vascular mucous membrane, inseparably united with the periosteum and perichondrium over which it lies. It is continuous with the skin through the nostrils; with the mucous membrane of the pharynx through the posterior nares; with the conjunctiva through the nasal duct and lachrymal canaliculi; and with the lining membrane of the several sinuses which communicate with the nasal fossæ. The pituitary membrane, however, varies much in thickness and vascularity in

different parts. It is thickest and most vascular over the turbinate bones (particularly the inferior) and on the septum nasi it is also very thick and spongy; but in the intervals between the turbinate bones, and over the floor of the nasal fossæ, it is considerably thinner. In the maxillary, frontal, and sphenoidal sinuses, and in the ethmoidal cells, the lining mucous membrane is very thin and pale, and contrasts strongly with that which lines the nasal fossæ.

The character of the epithelium varies in different parts, and by this in a general way, three regions of the nasal fossæ may be distinguished. Thus, the region of the external nostrils (the vestibule), including all the part which is roofed by the nasal cartilages, is lined with stratified squamous epithelium; and the remainder is divisible into two parts, viz.,

Fig. 413.

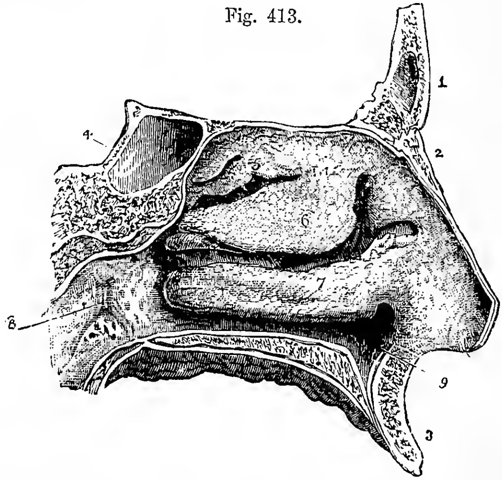


Fig. 413.—Outer wall of the left nasal fossa, covered by the pituitary membrane (Arnold). $\frac{3}{4}$

1, frontal bone; 2, left nasal bone; 3, superior maxillary; 4, body of the sphenoid with the sphenoidal sinus; 5, projection of the membrane covering the upper spongy bone; 6, that of the middle; 7, that of the lower; the upper, middle, and lower meatuses are seen below the corresponding spongy bones; 8, opening of the Eustachian tube; 9, depression of the lining membrane of the nose in the anterior palatine canal.

the upper or olfactory region in which the epithelium is non-ciliated and columnar, and the lower or respiratory region in which, as also in the sinuses, it is ciliated and columnar. The membrane in the respiratory part covers the inferior turbinate and all the lower portions of the fossæ, and is studded with numerous racemose glands (yielding in part mucus, in part a more watery secretion), which open by orifices apparent on the surface. They are most numerous about the middle and hinder parts of the nasal fossæ, and are largest at the back of the septum near the floor of the nasal cavity. Glands which are much smaller and less numerous open into the several cavities which communicate with the nasal fossæ. Besides the glands the membrane contains a variable amount of lymphoid tissue, occasionally accumulated into "nodules." In some parts large venous plexuses are found, encircled, as well as the alveoli of the glands amongst which they lie, by bundles of plain muscular fibres (Klein), thus forming a sort of cavernous tissue.

Olfactory mucous membrane.—The olfactory region or that in which the olfactory nerve is distributed, includes the upper and middle turbinate parts of the fossæ, and the upper portion of the septum. It is extremely vascular, a close plexus of large capillary vessels being found under the lining membrane throughout its whole extent. Its mucous membrane is thicker and more delicate in consistence than that of the ciliated region, being soft and pulpy. It has a distinct yellow colour in man; brown in some animals. The glands of this region (glands of Bowman) are numerous, but are of a more simple structure than those in the lower part of the fossæ. They open by fine ducts lined with flattened cells which extend to the surface between the olfactory epithelium-cells. In the mucous membrane itself, the gland-tube is somewhat convoluted and enlarged, and it may have one or two branches.

Fig. 414.

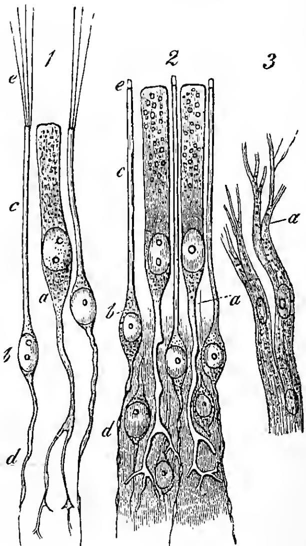


Fig. 414.—Cells and terminal nerve-fibres of the olfactory region (from Frey after Schultze). Highly magnified.

1, from the frog; 2, from man; *a*, epithelial cell, extending deeply into a ramified process; *b*, olfactory cells; *c*, their peripheral rods; *e*, their extremities, seen in 1 to be prolonged into fine hairs; *d*, their central filaments; 3, olfactory nerve-fibres from the dog; *a*, the division into fine fibrillæ.

It is limited throughout by a basement membrane, and lined and almost filled with columnar or polyhedral secreting cells. Here and there ordinary racemose glands are found; where this is the case the epithelium of the surface, according to Klein, is ciliated and not olfactory.

The columnar cells on the surface of the olfactory mucous membrane (fig 414, *a*) are prolonged at their deep extremities into a process which is generally somewhat thickened towards its deeper end, and usually includes a number of fatty granules; and from this thickened part branches proceed, which are stated by Exner and Martin to communicate with those of neighbouring cells, so as to form a communicating network throughout the extent of the membrane, underneath the epithelium. Amongst these branching central ends of the columnar cells there are a large number of peculiar spindle-shaped cells (fig. 414, *b*), each consisting of a large, clear nucleus surrounded by a relatively small amount of granular protoplasm. From each cell proceeds a superficial and a deep process. The superficial process (*c*) is a cylindrical or slightly tapering thread passing directly to the surface, and terminating abruptly at about the same level as the free surface of the epithelial cells between which it lies, or a little beyond; the deep process (*d*) is more slender, and passes vertically inwards. This last frequently presents a beaded appearance similar to that observed in fine nerve-filaments. These cells were termed by Max Schultze, *olfactory cells*, to distinguish them from the columnar epithelium-cells, which are much

fewer in number, and which are entirely surrounded with the fine rod-like peripheral processes of the smaller cells. It is probable that the fine varicose central processes of these cells are directly continuous with the fibrils of the olfactory nerve, but the continuity has never been actually observed. The nucleated bodies of the olfactory cells are several rows deep, and form a layer of considerable thickness beneath the columnar cells.

Both the olfactory and the columnar cells project through apertures in a cuticular lamina which bounds the mucous membrane superficially (*external limiting membrane* of v. Brunn).

The peripheral process of the olfactory-cell was observed by Schultze to be surmounted by a short projection (fig. 414. 2, *e*), but this appearance may result from the coagulation of albuminous matter escaped from the interior of the process. Long and fine hair-like processes do, however, exist on the olfactory-cells of amphibia, reptiles, and birds (fig. 414, 1, *e*), but they have not been observed in mammals.

According to Exner there is no sharp distinction between columnar and olfactory-cells, but intermediate forms are to be met with, and the olfactory-cells are, in fact, only a less developed condition of the columnar cells. He states that both kinds are connected with the olfactory nerve-fibres, that in the lower vertebrata they may both bear hair-like processes, and that in the frog, after removal of the olfactory lobes, they both disappear and give place to ordinary ciliated cells.

In the rabbit and guinea-pig Klein, in confirmation of a statement by Sidney, describes a lowermost layer of conical cells resting by their bases vertically upon the basement membrane.

Fig. 415.

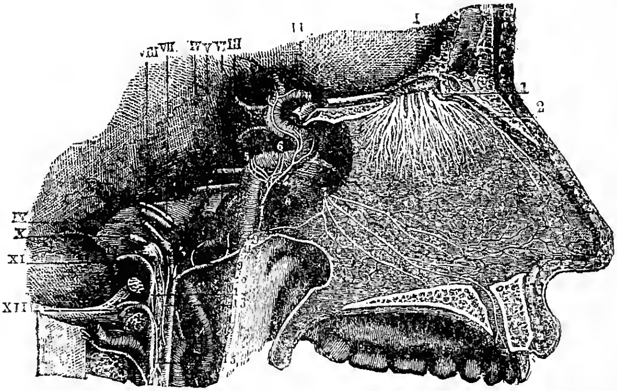


Fig. 415.—Nerves of the septum nasi, seen from the right side (from Sappey, after Hirschfeld and Leveillé). $\frac{2}{3}$

I, the olfactory bulb; 1, the olfactory nerves passing through the foramina of the cribriform plate, and descending to be distributed on the septum; 2, the internal or septal twig of the nasal branch of the ophthalmic nerve; 3, naso-palatine nerves.

Olfactory Nerve.—The filaments of this nerve, lodged at first in grooves on the surface of the bones, enter the substance of the Schneiderian membrane obliquely. The nerves of the septum (fig. 415) are rather larger than those of the outer wall of the nasal fossæ; they extend over the upper third of the septum, becoming very indistinct as they descend. The nerves of the outer wall are divided into two

groups—the posterior being distributed over the surface of the upper turbinate bone, and the anterior over the plain surface of the ethmoid and the middle turbinate bone.

The nerves ramify so as to form flattened tufts, the filaments of which, spreading out laterally and communicating freely with similar offsets on each side, form a close plexus, with elongated and narrow meshes.

Fig. 416.

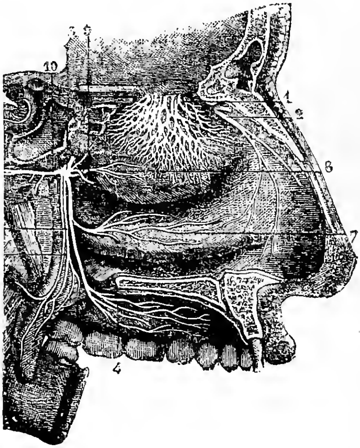


Fig. 416.—Nerves of the outer wall of the nasal fossæ (from Sappey, after Hirschfeld and Leveillé). $\frac{3}{5}$

1, network of the branches of the olfactory nerve, descending upon the region of the superior and middle turbinated bones ; 2, external twig of the ethmoidal branch of the nasal nerve ; 3, spheno-palatine ganglion ; 4, ramification of the anterior palatine nerves ; 5, posterior, and 6, middle divisions of the palatine nerves ; 7, branch to the region of the inferior turbinated bone ; 8, branch to the region of the superior and middle turbinated bones ; 9, naso-palatine branch to the septum cut short.

In their structure the olfactory nerve-fibres differ much from the ordinary dark-bordered fibres of the cerebral and spinal nerves : they possess no medullary sheath, but are axis-cylinders provided with a distinct nucleated sheath, much more distinct than that of the fibres of Remak and with nuclei at less frequent intervals (fig. 417).

Fig. 417.

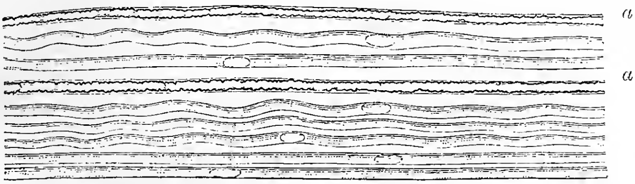


Fig. 417.—Nerve-fibres from the olfactory mucous membrane (Max Schultze).
Magnified between 400 and 500 diameters.
From a branch of the olfactory nerve of the sheep ; at *a*, *a*, two dark bordered or medullated fibres, from the fifth pair, associated with the pale olfactory fibres.

The greater part of the mucous membrane of the nasal fossæ is provided also with nerves of common sensibility, derived from branches of the fifth pair : the distribution of these has already been described in Vol. I.

The Organ of Jacobson.—In the anterior and lower part of the nasal septum a small aperture may be seen opening obliquely on to the surface of the mucous membrane slightly above and in front of the orifice of the Stenonian canal. This aperture leads into a minute canal which passes backwards for a short distance along the septum to terminate blindly a few millimeters from the orifice. The canal, which is lined with epithelium continuous with that of the nasal cavity and has numerous glands opening into it, is the homologue of a much

more extensively developed tubular organ which opens in a similar position in many quadrupeds, and is encircled by a special curved plate of cartilage which lies below the septal cartilage on either side and is known as the cartilage of Jacobson. This is only represented in man by a small narrow piece of cartilage (" the plough-share cartilage " of Huscke), which lies wholly below the rudimentary organ of Jacobson. In the rabbit and guinea-pig as shown by Klein, and probably in other animals in which the organ is in a well-developed condition, the epithelium which lines the inner or mesial side of the canal is much thicker than that on the outer side, and is similar in structure to that lining the olfactory part of the Schneiderian membrane. Moreover it receives considerable branches of the olfactory nerve, and in these animals is no doubt of high functional importance as an accessory to the proper organ of smell. For a further account, of this curious structure as well as references to the literature of the subject, see Kölliker, Ueber die Jacobson-schen Organe des Menschen, Leipzig, 1877 ; and a series of papers by Klein in the Quarterly Journal of Microscopical Science for 1881 and 1882.

Blood-vessels and lymphatics of the nasal fossæ. The *spheno-palatine branch of the internal maxillary artery* enters the cavity by the spheno-palatine foramen and divides into external branches to the meatuses and inner surface of the turbinate bones, sending offsets also to the ethmoidal cells and to the maxillary and frontal sinuses, and an internal branch (naso-palatine) along the septum to the incisor foramen.

The *descending palatine branch of the internal maxillary artery* gives small offsets to the hinder part of the inferior turbinate bone and meatus.

The *anterior ethmoidal branch of the ophthalmic artery* enters the cavity with the nasal nerve and is distributed to the mucous membrane of the fore part of the septum and outer wall.

The *posterior ethmoidal branch* of the same artery sends small twigs to the posterior ethmoidal cells, to the roof, and to the upper part of the septum.

Lastly the *artery of the septum* (from the superior coronary of the facial) supplies the part near the anterior nares. The several arteries anastomose freely together in the mucous membrane.

The *veins* form a dense plexus in the mucous membrane, and this is most largely developed over the lower turbinate bone, and on the lower and hinder part of the septum. The trunks leaving the cavity accompany the arteries, the *spheno-palatine vein* emptying itself into the pterygoid plexus ; the *ethmoidal veins* joining the ophthalmic, and small veins passing out at the margin of the nares to join the coronary vein of the upper lip. Some small veins also pierce the nasal bone and the ascending process of the superior maxilla to join the commencement of the facial vein.

The *lymphatics* are abundant and large. They form a close plexus in the mucous membrane, the branches extending almost to the surface, and a more open plexus of valved vessels nearer the bone. These are in communication with the lymphatic spaces which enclose the branches of the olfactory nerve, and these spaces again communicate with the subdural space of the cranium, so that the lymphatics of the nasal mucous membrane can be injected from the cranial cavity (Schwalbe).

Literature.—*M. Schultze*, Ue. d. Endigungsw. d. Geruchsnerven, &c., Berl. Acad., 1856 ; Halle Abhandl., 1863, and Med. Centralbl., 1864 ; *Exner*, in Wien. Sitzungsb., 1871, 1872, and 1877 ; *Grimm*, in Göttinger Nachr., 1872 ; *Babuchin*, in Stricker's Handb., 1872 ; *Langerhans*, in Freib. Ber., 1873 ; *Newell Martin*, in Journ. of Anat. and Phys., 1873 ; *Paschutin*, in Sächs. Ber., 1873 ; *Cisoff*, in Med. Centralbl., 1874 ; *v. Brunn*, in Med. Centralbl., 1874, and Arch. f. mikr. Anat., 1875 ; *Colosanti*, in Arch. f. Anat. u. Phys., 1875 ; *Föttinger*, in Bull. d. l'acad. d. Belg., 1876. All the above relate to the structure of the olfactory mucous membrane.

THE THORACIC VISCERA.

The greater part of the thorax is occupied by the lungs, each of which is invested by a serous membrane, the *pleura*. The heart, enclosed by a membranous covering, the *pericardium*, lies between the lungs in the middle of a space bounded laterally by the right and left pluræ, and known as the *mediastinal space* or simply as the *mediastinum*. The term *anterior mediastinum* is used to denote the part of this space immediately in front of the pericardium ; *middle mediastinum* that which contains and is filled by the pericardium ; and *posterior mediastinum* the part behind the pericardium ; whilst the upper part of the space, which is situated above the pericardium and extends as far as the root of the neck, may conveniently be distinguished as the *superior mediastinum*.

The **superior mediastinum** may be considered as bounded below by a plane passing through the lower part of the body of the fourth dorsal vertebra behind, and the junction of the manubrium with the body of the sternum in front. Its upper limit corresponds with the superior aperture of the thorax. In front are the manubrium and the lower ends of the sterno-hyoid and sterno-thyroid muscles ; and behind are the upper four dorsal vertebræ and the lower ends of the longus colli muscles. It contains the trachea, œsophagus and thoracic duct ; the whole of the transverse part of the arch of the aorta, the innominate artery, and those parts of the left common carotid and subclavian arteries which are contained within the thorax ; the innominate veins and upper part of the superior vena cava ; the phrenic and pneumo-gastric nerves, the left recurrent, and the cardiac nerves ; and the cardiac lymphatic glands and remains of the thymus gland.

The separate description of a superior mediastinum was suggested by Struthers (Journal of Anatomy, Vol. III.) and is manifestly convenient. The superior mediastinum as here defined is not identical however with that of Struthers, who makes the plane marking off the lower boundary pass a vertebra higher behind (although it is at the same level in front) and this puts the whole of the arch of the aorta into the middle mediastinum. The plane proposed by Struthers does not, however, in the majority of cases pass above the arch, but cuts off the upper part of its transverse portion, and it has also the disadvantage of being so oblique that the superior mediastinum cannot properly be said to be the part behind the manubrium. On the other hand the plane here proposed is nearly horizontal, and in the average condition passes just under the transverse portion of the arch, and this coincides with the extent upwards of the pericardium ; and is just above the roots of the lungs.*

The **anterior mediastinum** is narrow in its upper half, the two pleuræ coming nearly or quite into contact behind the second piece of the sternum. Below it is broader, the left pleura receding from its fellow, and is bounded in front by the sternum with the fifth and sixth, and a small portion of the seventh left costal cartilages, and by the triangularis sterni muscle ; behind it is the pericardium. This space contains only some areolar tissue, and in its lower part two or three small lymphatic glands (anterior mediastinal glands).

The **middle mediastinum** is the enlarged central portion of the whole space, containing in addition to the pericardium with its contents

* The above account of the superior mediastinum has been furnished by Professor Thane. (E.A.S.)

(viz., the heart, ascending portion of the arch of the aorta, trunk of the pulmonary artery and the lower half of the superior vena cava), the phrenic nerves and accompanying vessels, the arch of the azygos vein, and the roots of the lungs with the bronchial lymphatic glands.

The **posterior mediastinum** is the space between the pericardium and the roots of the lungs in front and the spine behind (from the lower border of the fourth dorsal vertebra downwards), the lateral boundaries being, of course, formed by the pleuræ. It contains the descending portion of the arch and the descending thoracic aorta ; the œsophagus with the pneumo-gastric nerves, the azygos veins, the thoracic duct and the posterior mediastinal lymphatic glands.

THE PERICARDIUM.

This membranous sac, in which the heart is contained, is of a somewhat conical shape, its base resting on the diaphragm, whilst the upper

Fig. 418.

Fig. 418.—Transverse section of the chest of a fœtus, on a level with the interval in front between the fifth and sixth ribs (Allen Thomson after Luschka).

The sketch represents the upper surface of the lower section ; the division is carried nearly in a horizontal plane. *s*, sternum ; *c*, body of the seventh dorsal vertebra ; *h*, right, and *h'*, left ventricle ; *œ*, œsophagus ; *p n*, left pneumogastric nerve ; the right pneumogastric nerve is behind the œsophagus ; *phr*, phrenic nerves ; *a*, aorta ; *v a*, vena azygos ; *d*, thoracic duct ; 1, 1, the cardiac pericardium ; 2, in the anterior mediastinal space, the parietal pericardium ; 2', 2', cavity of the pericardium ; 3, 3, pulmonary pleuræ passing over the surface, and reflected at the roots of the lungs, *r*, *r'* ; 3', 3', the pleural cavities, reflected in front at the mediastinum to the surface of the pericardium ; 4, 4, parietal pleuræ ; *c*, *c*, walls of the chest inclosing the ribs, pectoral muscles, &c.

narrower part surrounds the trunks of the great vessels. It consists of two layers, one external and fibrous, the other internal and serous.

The **fibrous** layer is a dense, unyielding membrane, consisting of fibres which interlace in every direction. This layer is attached below to the upper surface of the diaphragm (fig. 419, D), partly to the central tendon, partly to the adjoining muscular surface, especially on the left

Fig. 419.

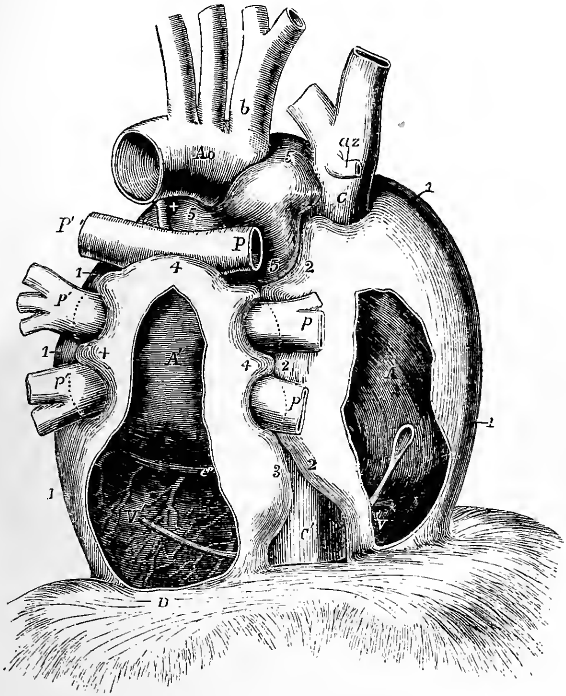


Fig. 419.—SEMI-DIAGRAMMATIC VIEW OF THE PERICARDIUM FROM BEHIND, DESIGNED TO SHOW THE PRINCIPAL INFLECTIONS OF THE SEROUS SAC ROUND THE GREAT VESSELS (Allen Thomson). $\frac{1}{2}$

The drawing is taken from preparations in which the heart and vessels had been partially filled by injection, the pericardium inflated and dried in the distended state, and the fibrous continuation on the vessels removed. By the removal of a portion of the pericardium from behind the right and left cavities of the heart, the position of that organ is made apparent. *A*, right auricle ; *A'*, left auricle ; *V*, right ventricle ; *V'*, left ventricle ; *Ao*, aortic arch ; *b*, innominate artery ; *C*, vena cava superior ; *az*, azygos vein ; *C'*, vena cava inferior ; *c''*, great coronary vein ; +, cord of the ductus arteriosus ; *P*, right, *P'*, left pulmonary artery ; *p*, right, *p'*, left pulmonary veins ; *D*, central tendon of the diaphragm ; 1, sac of the pericardium ; 2, the portion on the right side which partially surrounds the vena cava superior, the right pulmonary veins, and the vena cava inferior ; 3, portion on the left side which partially surrounds the vena cava inferior ; 4, portion which is extended upwards behind the left auricle, and partially folds over the pulmonary arteries and veins, meeting between these different vessels the extensions of the sac from the right and left ; 5, tubular portion which completely surrounds the aortic and pulmonary arterial trunks. A bent probe is passed within the pericardium from behind the right auricle, in front of the vena cava inferior, to the back of the left ventricle, which may indicate the place where the large undivided sac of the pericardium is folded round that vein.

side. Near the median line the connection is very firm, the fibrous structures being continuous; elsewhere the attachment is more lax, and is effected mainly by areolar tissue. The pericardium is fixed also in front by two ligamentous bands which pass to it from the manubrium and ensiform process of the sternum (Luschka). The fibrous layer is continued above for some distance along the large blood-vessels in the form of tubular prolongations, which become gradually lost upon their external coats. The superior vena cava, the four pulmonary veins, the aorta, and the right and left divisions of the pulmonary artery, receive investments of this kind.

The **serous** layer of the pericardium not only lines the fibrous layer, but, like other serous membranes, is reflected on the surface of the viscus which it invests. It has, therefore, a visceral and a parietal portion. The parietal portion adheres firmly to the fibrous membrane. It is reflected and becomes continuous with the visceral portion a short distance along the great vessels, about 1 to $1\frac{1}{2}$ inches from the base of the heart. In passing along the aorta and pulmonary artery, it encloses those vessels in a common short tubular sheath (fig. 419, 5, 5). It is reflected also upon the superior vena cava (C), and on the four pulmonary veins (p, p'), and forms a deep recess behind, between the entrance of the right and left veins into the left auricle. The inferior vena cava (C′) receives only a very scanty covering of this membrane (3, 2), inasmuch as that vessel enters the right auricle almost immediately after passing through the diaphragm, and is only partially surrounded by a reflection of the pericardium in the narrow interval between these parts. None of the vessels, indeed, joining the heart, with the exception of the aorta and pulmonary artery where they are united together, receive a complete covering from the pericardium, or can be said to be entirely enveloped in the sac.

When the left pulmonary artery and subjacent pulmonary vein are separated, a fold of the pericardium will be seen between them, which has been termed by Marshall the "vestigial fold." It is formed by a duplicature of the serous layer, including areolar and fatty tissue, together with blood-vessels and nerves, and is from half to three-quarters of an inch in length, and from half to one inch deep. It extends from the left superior intercostal vein above the pulmonary artery downwards to the side of the left auricle, where it is lost in a narrow streak which crosses round the lower left pulmonary vein. This fold encloses a vestige of a *left* superior vena cava (duct of Cuvier), which exists in early embryonic life. (Marshall, "On the development of the great anterior veins in Man and Mammalia," Philosoph. Trans., 1850.)

The pericardium is in relation in front and behind with the mediastina and their contents. Anteriorly also it is covered by the pleuræ and to some extent by the lungs, except below, where it approaches the surface in the angular space to the left of the lower part of the sternum. At the sides it is in contact with the phrenic nerves, as well as with the pleuræ and their contained viscera. Its relations to the diaphragm and great vessels have been already noticed.

In structure the serous layer of the pericardium agrees with that of serous membranes generally, being formed of connective tissue containing a network of elastic fibres, blood-vessels and lymphatic vessels.

THE HEART.

The heart is a hollow muscular organ, divided by a longitudinal septum into a right and a left half, each of which is again subdivided by a transverse constriction into two compartments, communicating with each other, and named **auricle** and **ventricle**. Its general form is

that of a blunt cone. Enclosed, as before said, in the pericardium, it

Fig. 420.

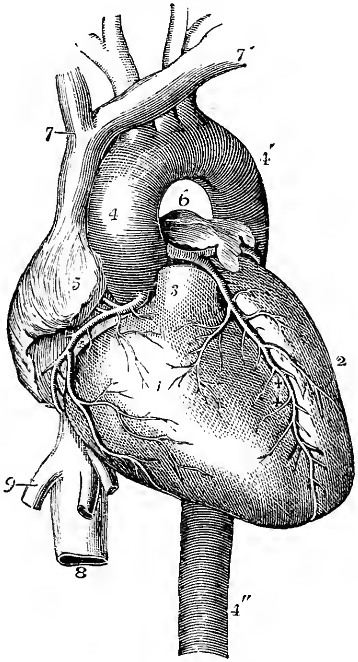


Fig. 420.—The heart and great vessels from before (R. Quain). $\frac{1}{3}$

The pulmonary artery has been cut short close to its origin in order to show the first part of the aorta. 1, right ventricle; 2, left ventricle; 3, root of the pulmonary artery; 4, 4′, arch of the aorta; 4″, the descending aorta; 5, the appendix and anterior part of the right auricle; 6, those of the left auricle; 7, 7′, innominate veins joining to form the vena cava superior; 8, inferior vena cava below the diaphragm; 9, one of the large hepatic veins; +, right; + +, left coronary artery.

is placed behind the sternum and the costal cartilages (fig. 430; on page 492), the broader end, or base being directed upwards, backwards, and to the right, and extending from the level of the fifth to that of the eighth dorsal vertebra; the apex downwards, forwards, and to the left. In the living subject its stroke against the wall of the chest is felt in the space between the cartilages of the fifth and sixth ribs, a little below and to the inner side of

Fig. 421.

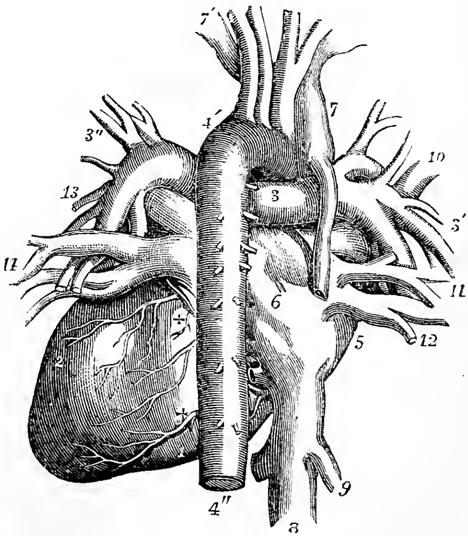


Fig. 421.—View of the heart and great vessels from behind (R. Quain). $\frac{1}{3}$

1, right ventricle; 2, left ventricle; 3, right pulmonary artery; 3′, its branches passing into the root of the right lung; 3″, the same of the left; 4′, arch of the aorta; 4″, descending aorta; 5, right auricle; 6, is placed on the division between the right and left auricles; 7, superior vena cava; 7′, left innominate vein; 8, inferior vena cava; 9, right hepatic vein; 10, 11, 12, right pulmonary veins; 13, 14, left pulmonary veins; +, +, branches of the right and left coronary arteries.

the left nipple ($3\frac{1}{4}$ inches from the middle line of sternum and $1\frac{1}{2}$ inch below the nipple): in the dead body the apex is a little higher than during life. The heart, therefore, has a very

oblique position in the chest, and projects farther into the left than into the right half of the cavity. Its position is affected to a certain extent by that of the body; thus it comes more into contact with the anterior wall of the chest when the body is in the prone posture or is lying on the left side. In inspiration, on the other hand, when the diaphragm sinks and the lungs expand, it recedes slightly from the chest-wall.

The heart is attached at its base to the great blood-vessels, and the serous layer of the pericardium is here continued on to it. Otherwise the heart is entirely free within the sac of the pericardium. The convex anterior surface looks somewhat upwards as well as forwards towards the sternum and costal cartilages: from these it is for the most part separated by the pleuræ. The lungs also advance over it to some extent, and encroach still farther during inspiration, so as in that condition to leave only a triangular part, not more than two square inches in extent, uncovered.* The posterior or under surface is flattened, and rests on the diaphragm. Of the two borders or margins formed by the meeting of the anterior and posterior surfaces, the right or lower border, called *margo acutus*, is comparatively thin, and is longer than the upper or left border, which is more rounded and is named *margo obtusus*.

A deep transverse groove, the *auriculo-ventricular furrow*, divides the heart into the auricular and the ventricular portions; and on the ventricular portion two *longitudinal furrows*, situated one on the anterior, the other on the posterior surface, mark its division into a right and left chamber. They extend from the base of the ventricular portion, and are continuous one with the other a little to the right of the apex, which is thus formed entirely by the wall of the left ventricle. The anterior longitudinal furrow (fig. 420, + +) is nearer to the left, and the posterior furrow nearer to the right side of the heart, the right ventricle forming more of the anterior, and the left more of the posterior surface of the organ. In the furrows run the coronary arteries and veins with lymphatic vessels and nerves, embedded in fatty tissue and covered by the visceral layer of the pericardium.

CAVITIES OF THE HEART.

The heart, as before remarked, contains four chambers or compartments, a right and a left auricle and a right and a left ventricle.

The **right auricle** (fig. 420, 5) is best brought into view on turning the heart somewhat to the left side; it is then seen to occupy the right and anterior portion of the base of the organ. When thus viewed the auricle appears of a quadrangular form, the superior and inferior venæ cavæ, occupying respectively the upper and lower posterior angles, while a tongue-shaped portion, the *auricular appendix* or *auricle proper*,† is seen to project from the anterior and upper angle and to turn to the left over the root of the aorta. The main part of the auricle, that into which the great veins directly pour their blood, is commonly named *sinus venosus* or *atrium*, to distinguish it from the auricular appendix. When opened, the interior of the right auricle presents a smooth and

* This uncovered part may be marked off on the surface of the chest by two lines drawn from the point of the apex-beat to the middle line of the sternum, one horizontal, the other extending obliquely upwards to between the fourth cartilages.

† So termed from its resemblance to the external ear of some animals.

even surface, except in the appendix which is ridged vertically with closely set reticulated muscular bands, and upon the anterior wall of the sinus, where similar bundles are seen extending, but here running parallel with one another, like the teeth of a comb, and thence termed *musculi pectinati*.

The posterior wall corresponds with the partition between the two auricles (*septum auricularum*). Near its lower part and just above and to the left of the orifice of the inferior vena cava is an oval depression, the *fovea* or *fossa ovalis* (fig. 422, 3′), the remains of the *foramen ovale*

Fig. 422.

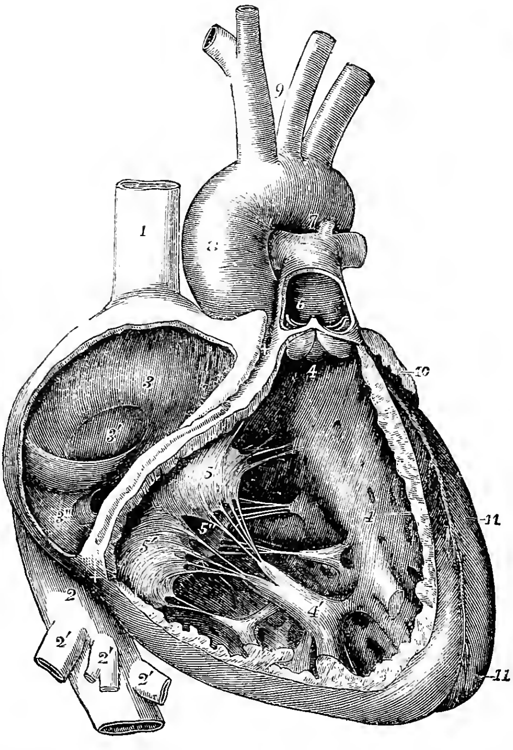


Fig. 422.—Interior of the right auricle and ventricle, exposed by removal of a part of their right and anterior walls (Allen Thomson). $\frac{1}{2}$

1, superior vena cava; 2, inferior vena cava; 2′, hepatic veins; 3, septum of the auricles; 3′, fossa ovalis, the Eustachian valve is just below; 3″, aperture of the great coronary vein with its valve; +, +, auriculo-ventricular groove, a narrow portion of the adjacent walls of the auricle and ventricle having been preserved; 4, 4, on the septum, the cavity of the right ventricle; 4′, large anterior papillary muscle; 5, left; 5′, right, and 5″, posterior or septal segment of the tricuspid valve; 6, pulmonary artery, a part of the anterior wall of that vessel having been removed, and a narrow portion of it preserved at its commencement where the pulmonary valve is attached; 7, concavity of the aortic arch close to the cord of the ductus arteriosus; 8, ascending part of the arch covered at its commencement by the auricular appendix and pulmonary artery; 9, placed between the innominate and left common carotid arteries; 10, appendix of the left auricle: 11, 11, left ventricle.

(*vestigium foraminis ovalis*), which is an open passage in the fœtal heart from the right to the left auricle. The *fossa ovalis* is bounded above and at the sides by a prominent border, deficient below, the *annulus ovalis* or *isthmus Vieussenii*, whilst the floor of the fossa, formed by what was previously a valve, is thin and translucent; and occasionally a small oblique passage leading into the left auricle is left between it and the annular border. At the right part of the cavity are seen the orifices of the superior and inferior venæ cavæ, the ~~former~~ passing downwards and forwards, the ~~latter,~~ the larger, being directed upwards and latter former

inwards. Between the two orifices is a slight projection, better marked in certain quadrupeds than in man, which has received the somewhat misleading name of *tubercle of Lower.*

In front of the orifice of the inferior vena cava, and partly covering it, is a crescentic fold of the lining membrane, the *Eustachian valve*, which is continuous by its convexity with the margin of the venous orifice, while its anterior cornu is prolonged into the anterior limb of the annulus ovalis. This valve, which is very variable in character in the adult, being often cribriform or perforated with holes, is an important structure in the fœtal heart, and serves the purpose of directing the stream of blood from the inferior vena cava through the foramen ovale into the left auricle. The other openings into the right auricle are 1,—the *auriculo-ventricular aperture*, situated in front of the inferior vena cava and occupying the anterior and under part of the cavity: it is oval in form and large, admitting three fingers easily; 2, the *orifice of the coronary sinus* of the heart (fig. 422, 3″), situated between the inferior cava and the auriculo-ventricular opening: this is guarded by a semicircular valve, sometimes double, which, although previously figured by Eustachius, is often named valve of Thebesius; 3, *openings of* two or three *anterior cardiac veins* from the surface of the right ventricle; and 4, the *foramina of Thebesius,* a number of small pits variously situated, some of which are merely recesses closed at the bottom, whilst others are the mouths of small veins (*venæ minimæ cordis*).

According to L. Langer the foramina Thebesii are not confined to the right auricle but occur in all the cavities of the heart; and into some of them, even in the ventricles, small veins which proceed from the muscular substance of the heart open.

Fig. 423.

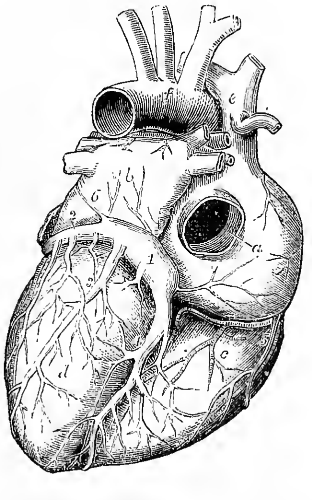


Fig. 423.—View of the adult heart, from behind, to show the coronary veins (Allen Thomson). $\frac{1}{3}$

a, placed on the back of the right auricle, points to the Eustachian valve seen within the opening of the inferior vena cava; *b*, left auricle; *c*, right ventricle; *d*, left ventricle; *e*, vena cava superior; *f*, arch of the aorta; 1, coronary sinus; 2, great coronary vein turning round the heart in the auriculo-ventricular groove; 3, posterior cardiac veins; 4, middle cardiac vein; 5, one of the anterior cardiac veins passing directly into the right auricle; 6, the vestige of the left superior vena cava proceeding over the left auricle downwards to join the coronary sinus.

The coronary vein (fig. 423, 1) is considerably dilated before it enters the auricle, and this dilated portion, which is embedded in the posterior wall of the left auricle, is termed the "coronary sinus." At the junction of the coronary vein with the dilated portion there is a valve consisting of one or two segments. Other small veins likewise enter the coronary sinus, each of them protected by a valve. One of these small veins, the "oblique vein" of Marshall (fig. 423, 6), takes a straight course from the vestigial fold before mentioned, over the back of the left auricle, to open into the coronary sinus. This vein has no valve

over its orifice: it, together with the coronary sinus, is to be looked upon as the remnant of the original left superior vena cava of the embryo (vide antea, p. 480).

The **right** or **anterior ventricle** (fig. 420, 1) occupies the chief part of the anterior surface of the heart, the right border, and a smaller portion of the posterior surface. It extends nearly, but not quite, to the apex. The upper and left angle is prolonged in a conical form to the commencement of the pulmonary artery: this part of the ventricle is named *conus arteriosus*, or *infundibulum*. The muscular wall of this ventricle is thickest at the base, and becomes thinner towards the apex. When the cavity is laid open (fig. 422) the septum of the heart is seen to bulge into it, so that in cross section this ventricle is crescentic in form (fig. 424, 6). At the base of the ventricle are two orifices, protected by valves; the *auriculo-ventricular*, of an oval form, and situated towards the right, and that of the *pulmonary artery*, smaller, more elevated, and towards the left. Between the two the wall of the cavity projects downwards, in the form of a thick

Fig. 424.

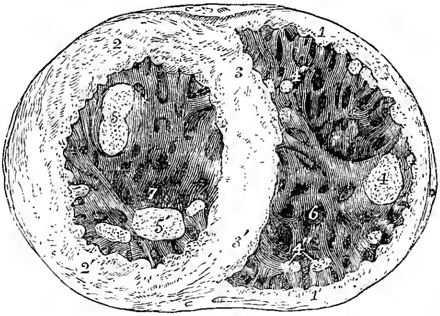


Fig. 424.—Cross Section of the Ventricular part of the Heart at two-thirds from the Apex looking downwards into the Cavities (Allen Thomson). $\frac{2}{3}$

1, 1′, Wall of the right ventricle; 2, 2′, wall of the left; 3, 3′, septum; 4, the principal papillary muscle of the right ventricle; 4′, some columnæ carneæ on the septum near the front; 4″, others posteriorly near the septum; 5, 5′, the principal papillary muscles of the left ventricle; 6, the deepest part of the cavity of the right ventricle; 7, that of the left ventricle at the apex of the heart.

rounded muscular partition. The inner surface is marked by muscular bundles, "columnæ carneæ," some of which are attached by each extremity to the wall of the ventricle and are free in the middle, others are only sculptured in relief, as it were, being continuous with the wall of the ventricle in their whole length; while a third set, forming two principal bundles, an anterior and a posterior, named *musculi papillares*, are connected at their base with the ventricular wall, and by the other end are attached to small tendinous cords (*chordæ tendineæ*), through which they are connected with the segments of the auriculo-ventricular valve. The inside of the conus arteriosus is smooth, and free from columnæ carneæ.

The valve guarding the right auriculo-ventricular opening is composed of three triangular segments, or flaps (right, left or infundibular, and posterior or septal), and is hence named the *tricuspid*. The flaps are mainly formed of fibrous tissue covered by endocardium. At their bases, they are continuous with one another, so as to form an annular membrane attached around the margin of the auricular opening: they are directed downwards, and are retained in position within the ventricle by the chordæ tendineæ, which are attached to their ventricular surfaces and free margins. The middle part of each seg-

ment is thicker than the rest, whilst the marginal part is thin, transparent, and jagged at the edges (compare fig. 428, B, *e*, *e′*).

The chordæ tendineæ from the anterior papillary muscle pass to the cleft between the right and left segments, to be attached to both: the chordæ tendineæ from the posterior papillary muscle are attached in like manner to the right and posterior segments; while others forming a third set spring directly from the surface of the septum, sometimes from small eminences upon it, and pass upwards to be attached to the adjacent borders of the left and posterior segments.

During the contraction of the ventricle, the segments of the valve are applied to the opening leading from the auricle, and prevent the blood from rushing back into that cavity. Being retained by the chordæ tendineæ, the expanded flaps of the valve resist the pressure of the blood, which would otherwise force them back through the auricular orifice; the papillary muscles, shortening as the cavity of the ventricle itself shortens, prevent the valve from yielding too much towards the auricle. In the angles between each pair of the principal segments of the auriculo-ventricular valves there may be found, but not constantly, as many small intermediate lobes.

According to Kürschner (Wagner's Handwörterbuch, art. "Herzthätigkeit"), there are three kinds of cords to each segment; *a*, the first set generally two to four in number and proceeding from two different sets of papillæ, or from one of these and the wall of the ventricle, run to the attached margin of the segment, and are there connected also with the tendinous ring round the auriculo-ventricular opening; *b*, the second set, more numerous, and smaller than the first, proceed also from two adjacent papillary muscular groups, and are attached at intervals to the back or ventricular surface of each segment along two or more lines extending from the points of attachment of the tendons of the first order at the base of the valve to near its free extremity; *c*, the third set, which are still more numerous and much finer, branch off from the preceding ones, and are attached to the back and edges of the thinner marginal portions of the valves. A few muscular fibres prolonged from the neighbouring walls of the auricles penetrate into the segments of the auriculo-ventricular valves; blood-vessels accompany these but in all other parts the valves are non-vascular (L. Langer).

A fibrous band, sometimes muscular, is often found stretching across the cavity of the right ventricle from the base of the anterior papillary muscle to the septum. It represents the strong "moderator" band found in the heart of the ox, and of some other mammals, and in that of birds (Rolleston).

The valve at the orifice of the pulmonary artery consists of three flaps, a right and left and a posterior, named from their shape *semilunar* or *sigmoid* (fig. 422; fig. 427, I): they are constructed similarly to those on the left side at the root of the aorta: and as the characters of the last named are better marked, the more complete description will be reserved until these are treated of.

The **left auricle** occupies the left and posterior part of the base of the heart. The atrium presents from behind, where it is best seen, a quadrilateral appearance (fig. 423, *b*). In front it is in contact with the aorta and pulmonary artery; behind, it receives two pulmonary veins on each side, those from the left lung entering very close together; on the right, it is in contact with the other auricle. The *auricular appendage* (fig. 420, 6) is the only part of the left auricle seen from the front: it extends forwards from the left side of the atrium, and curves towards the right side, resting on the pulmonary artery. It is more curved as well as longer and narrower than that of the right auricle, and its margins are more deeply indented.

The interior of the appendix presents musculi pectinati somewhat similar to those in the right side of the heart, but the walls of the sinus

venosus are altogether smooth and even, and are also thicker than those of the right auricle. Posteriorly the openings of the pulmonary veins are seen, usually two on each side, and without valves (fig. 425, 1). The two veins of one or both sides sometimes unite into one before entering the auricle, whilst in other cases there is found an additional opening,

Fig. 425.

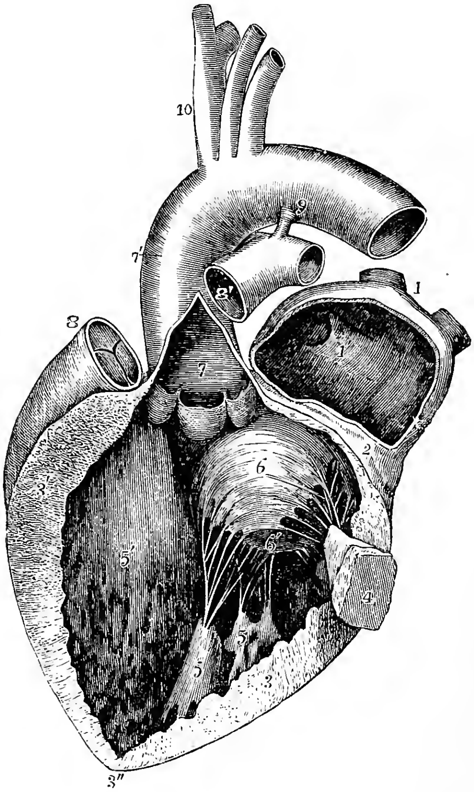


Fig. 425.—The left auricle and ventricle opened and a part of the wall removed so as to show their interior. (Allen Thomson). ½

The commencement of the pulmonary artery has been cut away, so as to show the aorta: the opening into the left ventricle has been carried a short distance into the aorta between two of the semilunar flaps; part of the auricle with its appendix has been removed. 1, the two right pulmonary veins cut short; 1′, placed within the cavity of the auricle on the left side of the septum and on the part which forms the remains of the valve of the foramen ovale, of which the crescentic border is seen; 2′, a narrow portion of the wall of the auricle and ventricle preserved around the auriculo-ventricular orifice; 3, 3′, cut surface of the wall of the ventricle, seen to become very much thinner towards 3″, at the apex; 4, a small part of the wall of the left ventricle which has been preserved with the left papillary muscle attached to it; 5, 5, right papillary muscles; 5′, the left side of the septum ventriculorum; 6, the anterior or aortic segment, and 6′, the posterior or parietal segment of the mitral valve; 7, placed in the interior of the aorta near its commencement and above its valve; 7′, the exterior of the great aortic sinus; 8, the upper part of the conus arteriosus with the root of the pulmonary artery and its semilunar valves; 8′, the separated portion of the pulmonary artery remaining attached to the aorta by 9, the cord of the ductus arteriosus; 10, the arteries rising from the summit of the aortic arch.

most frequently on the right side. In the lower and fore part of the auricle is situated the left *auriculo-ventricular* orifice. It is of an oval form, and is rather smaller than the corresponding opening between the right auricle and ventricle. On the septum between the auricles, a lunated depression may be observed (1′), comparable to a mark made by the finger-nail on a soft surface. This is the vestige of the foramen ovale, as it appears on the left side. The depression is limited by a slight crescentic ridge, the concavity of which is turned upwards, and

which is in fact the border of the now adherent membranous valve, which during fœtal life is applied to the left side of the then open foramen ovale. The line of adhesion may vary so as to leave more or less of a pocket-like recess.

The **left** or **posterior ventricle** occupies the left border of the heart, but only about a third of its extent appears on the anterior surface, the rest being seen behind. It is longer and narrower than the right ventricle, and the cross section of its cavity is oval, not crescentic, the septum on this side being concave (fig. 424). Its walls, which excepting near the apex, are nearly three times as thick as those of the right ventricle, are thickest at the part where the ventricle is widest, about one-fourth of its length from the base (fig. 425, 3) ; from this point they become thinner towards the auricular opening, and still thinner towards the apex (3″), which is, therefore, the weakest part. The lining membrane, which is continuous with that of the left auricle and the aorta, is usually less transparent than that of the right ventricle, especially in later life. In the interior of the cavity are noticed columnæ carneæ, musculi papillares with chordæ tendineæ, and two orifices guarded with valves. The *columnæ carneæ* are smaller than those of the

Fig. 426.

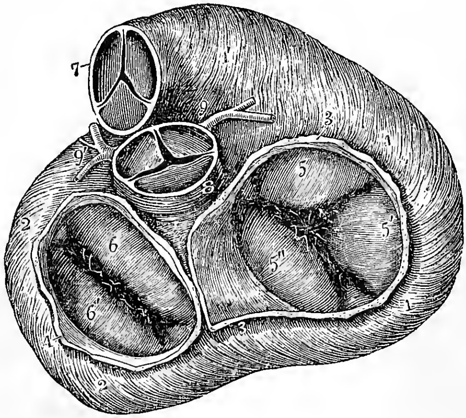


Fig. 426.—View of the base of the ventricular part of the heart, showing the relative position of the arterial and auriculo-ventricular orifices (Allen Thomson). $\frac{2}{3}$

The muscular fibres of the ventricles are exposed by the removal of the pericardium, fat, bloodvessels, &c. ; the pulmonary artery and aorta and the auricles have been removed. The valves are in the closed condition. 1, 1, right ventricle ; 1′, conus arteriosus ; 2, 2, left ventricle ; 3, 3, the divided wall of the right auricle ; 4, that of the left ; 5, the left, 5′, the right, and 5″, the septal segment of the tricuspid valve ; 6, the anterior or aortic, and 6′, the posterior or parietal segment of the mitral valve (in the angles between these segments are seen smaller fringes) ; 7, the pulmonary artery ; 8, placed upon the root of the aorta ; 9, the right, 9′, the left coronary artery.

right ventricle, but are more numerous and more closely reticulated. Their intersections are very numerous near the apex of the cavity, and also along its posterior wall, but the upper part of the anterior wall and septum is comparatively smooth. The *musculi papillares* (4, 5) are col-

lected into two groups, which are larger than those of the right ventricle. The two orifices of this ventricle are situated very close together, with one of the segments (fig. 426, 6) of the auriculo-ventricular valve between: the auricular opening is placed at the left and posterior part of the base of the ventricle; the aortic opening, in close proximity in front and towards the right.

The *bicuspid* or *mitral* valve (fig. 426, 6 6′), at the left auricular opening, resembles in structure the tricuspid valve of the right ventricle, but it is much thicker and stronger in all its parts, and consists of only two pointed segments, continuous at their attached bases. The larger of the two segments is suspended obliquely to the right and in front of the other, between the auricular and aortic openings: the smaller to the left and behind, and close to the wall of the ventricle. There is usually a smaller lobe at each angle of junction of the two principal segments, more apparent than those between the segments of the tricuspid valve.

As on the right side, the two sets of chordæ tendineæ from the papillary muscles proceed each to an angle between the two segments, and are attached in like manner to their margins and ventricular surfaces (fig. 426, and fig. 428 B, *e*), so that the musculi papillares, when they contract, tend to bring the edges of the flaps together. The chordæ tendineæ are stronger and less numerous than in the right ventricle. Small bands, partly muscular partly tendinous, may often be found crossing the cavity of the ventricle in various directions. They appear to be vestiges of the spongy structure of the cavity during a part of embryonic life.

The arterial or *aortic orifice* circular in form, and smaller than the auricular, is separated from it only by the attachment of the anterior segment of the mitral valve. As in the pulmonary artery, its valve consists of three semicircular flaps (*semilunar* or *sigmoid*,) (fig. 427, II) each of which is attached by its convex border to the side of the artery

Fig. 427.

I II

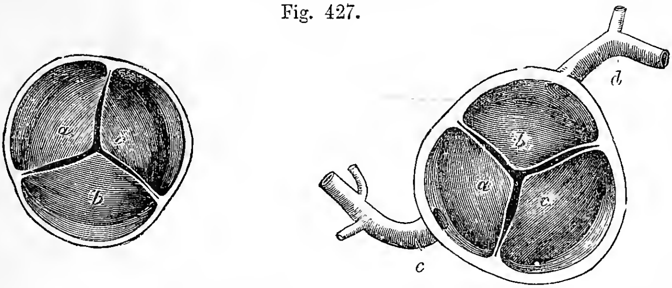


Fig. 427.—The semilunar valves of the aorta and pulmonary artery, seen from their distal side (Allen Thomson).

I, transverse section of the pulmonary artery immediately above the attachment of the semilunar valves: *a*, the left, and *c*, the right anterior segments; *b*, the posterior segment: opposite each the sinus of Valsalva is seen, and the attachment of the valve-segments to the inner wall of the artery.

II, a similar section of the aorta: *a*, the left posterior segment, *b*, the anterior segment, with the corresponding sinuses of Valsalva, from which the coronary arteries are seen to take their origin; *c*, the right posterior segment; *d*, the right, and *e*, the left coronary arteries.*

* It would appear that the above nomenclature most correctly describes the relative position of the valve-segments. Those of the pulmonary valve are often, however, spoken of as an anterior, *a*, and two posterior; and those of the aortic, as a posterior, *c*, and two anterior.

at the place where it joins the ventricle, whilst its other border, nearly straight, is free, and projects into the interior of the vessel.

Fig. 428.

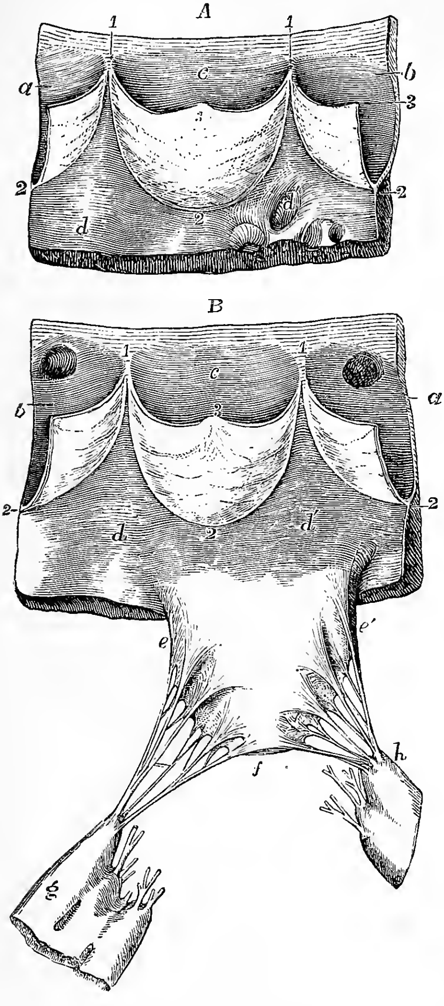


Fig. 428.—Views of parts of the semilunar and mitral valves, as seen from within the ventricle (Allen Thomson).

A, portion of the pulmonary artery and wall of the right ventricle with one entire segment and two half segments of the valve; *a*, *b*, *c*, sinuses of Valsalva opposite the segments; *d*, *d′*, inner surface of the ventricle; 1, 2, curved attached border of the segments; 3, the middle of the free border (corpus Arantii).

B, portion of the aorta and wall of the left ventricle with one entire segment and two half segments of the aortic valve, and the right or anterior segment of the mitral valve; *a*, *b*, *c*, sinuses of Valsalva opposite the segments; in *a*, and *b*, the apertures of the coronary arteries are seen; *d*, *d′*, the inner surface of the wall of the ventricle; 1, 2, and 3, as before; *e*, *e′*, the base of the anterior segment of the mitral valve; *f*, its apex; between *e*, and *e′*, and *f*, the attachment of the branched chordæ tendineæ to the margin and outer surface of the valve segment; *g*, right, *h*, left principal papillary muscle: the cut chordæ tendineæ are those which belong to the posterior segment and the small or intermediate segments.

The segments of these valves are composed of fibrous tissue covered by a prolongation of the endo-cardium on the one side, and of the inner coat of the artery on the other side. Their thickness varies at different parts. A tendinous band strengthens the free edge of the valve, and at the middle of that margin there is a slight fibro-cartilaginous thickening, the *nodulus* or *corpus Arantii* (fig. 428, 3). Other tendinous fibres, arising from the attached border, run in the valve towards the nodule: occupying its whole extent, except two narrow lunated portions, one on each side, adjoining the free margin of the valve. These parts, which are named *lunulæ*, are therefore thinner than the rest. There is also a strengthening fibrous cord surrounding the attached border of each valve. The wall both of the aorta and pulmonary artery is bulged out opposite each semilunar flap: these bulgings are known as the *sinuses of Valsalva*. In the aorta these are situated one anteriorly and two posteriorly (right and left). From the anterior arises the right coronary artery; from the left

posterior the left coronary artery: these vessels being for the supply of blood to the substance of the heart.

Fig. 429.

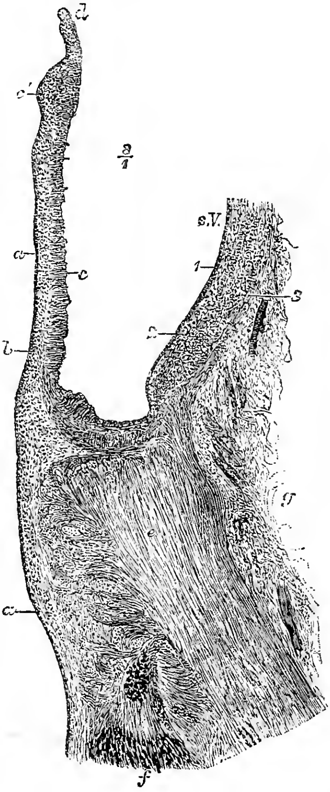


Fig. 429.—Section through one of the flaps of the aortic valve, and part of the corresponding sinus of Valsalva, with the adjoining part of the ventricular wall. (V. Horsley.) $\frac{8}{1}$.

a, endocardium, prolonged over the valve; *b*, subendocardial tissue; *c*, fibrous tissue of the valve, thickened at *c'* near the free edge; *d*, section of the lunula; *e*, section of the fibrous ring; *f*, muscular fibres of the ventricle attached to it; *g*, loose areolar tissue at the base of the ventricle; *s. V.*, sinus Valsalvæ: 1, 2, 3, inner, middle, and outer coats of the aorta.

The capacity of the sinuses of Valsalva is greater, and the tendinous tissue in the valves is more strongly marked at the mouth of the aorta than at the commencement of the pulmonary artery.

The part of the left ventricle adjoining the root of the aorta forms a small compartment, the "*aortic vestibule*" of Sibson, the walls of which are fibrous, or, in some parts, fibro-cartilaginous, so that it remains uncollapsed, and allows space for the bulging flaps of the aortic valve to descend during diastole.

POSITION OF THE PARTS OF THE HEART WITH RELATION TO THE WALL OF THE THORAX.

Nearly two-thirds of the bulk of the heart lie to the left of the middle line (fig. 430). The *right auricle* (3′) lies behind the sternal ends of the third, fourth and fifth costal cartilages, and the intervening portions of the intercostal spaces, and is also partly covered by the right edge of the sternum. The point of its auricular appendage is exactly behind the middle line on a level with the upper border of the third costal cartilages (3). The *left auricle* extends vertically from the level of the lower border of the second left cartilage to the upper border of the fourth (sternal end); and in breadth corresponds to the body of the eighth dorsal vertebra and the head of the adjoining rib. The apex of its appendage (4) is in the lower part of the second intercostal space or behind the third costal cartilage, about an inch and a quarter from the left of the sternum. The *right ventricle* extends from above down from the third to the sixth cartilages on the left side. The conus arteriosus is its most projecting part, being uncovered by lung. The *auriculo-*

Fig. 430.

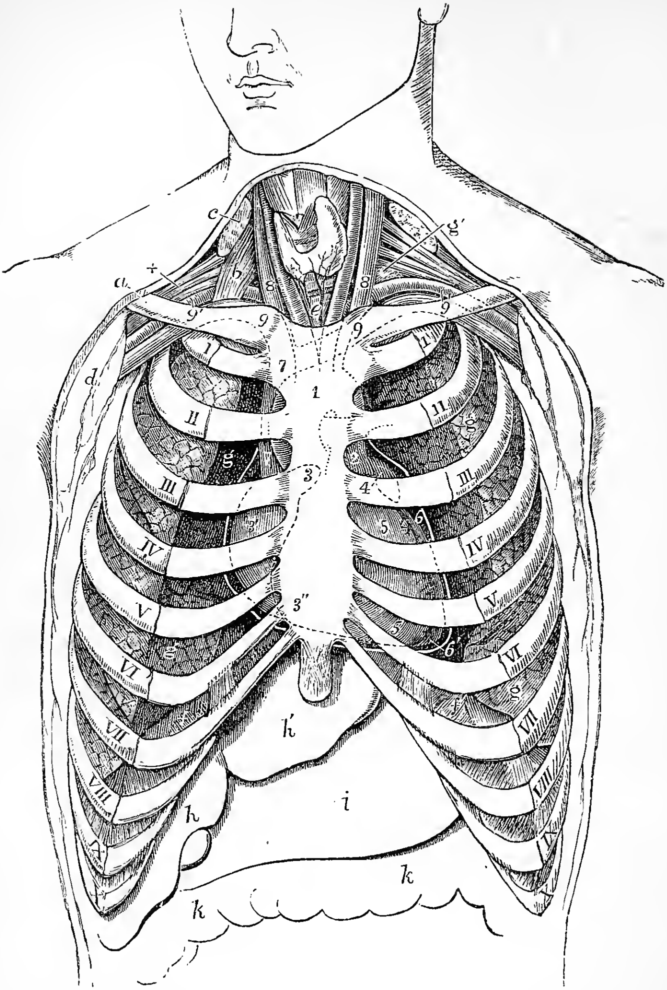


Fig. 430.—Semi-diagrammatic representation of the chest, to show the position of the heart and great vessels, as seen behind the sternum and costal cartilages (A. Thomson, modified from Luschka). $\frac{1}{4}$

The lungs have shrunk from the front of the chest. The heart is slightly higher than during life, and the aorta more to the right. *a*, right clavicle; *b*, scalenus anticus muscle; *c*, sterno-mastoid muscle divided; *d*, pectoral muscles divided; +, axillary nerves above the subclavian artery; *e*, trachea below the isthmus of the thyroid body; *f*, *f*, upper surface of the diaphragm; *g*, *g*, lungs; *g′*, on the left side, apex of the lung appearing in the neck; *h*, right, *h′*, left lobe of the liver; *i*, stomach; *k*, *k*, transverse colon; I, to X, first to tenth ribs near their cartilages; 1, placed on the lower part of the manubrium of the sternum, and over the arch of the aorta (indicated by dotted lines); 2′, placed in the second left intercostal space, on the stem of the pulmonary artery; 3, appendix of the right auricle; 3′, on the sinus venosus, behind the third space; 3″, its lower part at the junction of the sixth and seventh costal cartilages with the sternum; 4, left auricular appendix; 5, 5, right ventricle; 6, left ventricle;

6′, apex of the heart: the white line outside the heart is intended to indicate the external pericardium, as if the anterior half were removed by a transverse incision; 7, 7, vena cava superior; 8, 8, internal jugular veins; 9, 9, subclavian veins, joining the jugular; 9-7, 9-7, innominate veins; the right rising behind the sterno-clavicular articulation, the left crossing obliquely behind the upper half of the manubrium. The position of the first parts of the innominate artery, left carotid and left subclavian arteries, is indicated behind and below this vein; 9′, 9′, outer part of the subclavian arteries. It is to be observed that in this figure the attachment of the sixth costal cartilage to the sternum is represented a little too high.

ventricular sulcus corresponds with a line drawn obliquely upwards from near the sternal end of the sixth costal cartilage on the right side, to the third cartilage on the left. The *rounded margin* formed by the left ventricle extends on the left side from the third cartilage to a point in the fifth space two inches vertically below the nipple. The *sharp margin* formed by the right ventricle passes from the sternal end of the sixth cartilage on the right, and passes transversely behind the seventh right cartilage, the ensiform (at its upper third), and the seventh left cartilage, to meet the other margin at the apex.

The *apex of the heart* (fig. 430, 6′) is situated about $3\frac{1}{2}$ inches to the left of the middle line, in the fifth intercostal space, close to the upper margin of the sixth rib.

The *auriculo-ventricular openings* lie slightly to the left of the line of the auriculo-ventricular sulcus. The *right orifice* lies behind the sternum, on a level with the fourth intercostal space. The *left* is behind the left half of the sternum, on a level with the fourth costal cartilage. The *orifice of the pulmonary artery* is placed immediately to the left of the sternum, behind the edge of that bone and the third cartilage, and the pulmonary trunk extends up to the second left cartilage. The *aortic orifice*, also partly behind the left half of the sternum, is on a slightly lower level than the orifice of the pulmonary artery (being opposite the lower part of the third cartilage and the third intercostal space), and is covered by it in one-fourth its diameter. The aortic orifice is exactly behind the posterior wall of the conus arteriosus.

INTIMATE STRUCTURE OF THE HEART.

The heart is closely invested by a serous membrane, the cardiac pericardium (*epicardium*), and its cavities are lined by a smooth membrane, termed the *endocardium*, but the main substance of the organ is composed of muscular tissue (*myo-cardium*), with a certain amount of interstitial areolar tissue and numerous blood-vessels, lymphatics, and, in some parts, nerves and ganglia. There is also a considerable amount of fat chiefly collected at the base of the heart and beneath the pericardium, while in connection with the large orifices at the base of the ventricles a mass of fibrous tissue and fibro-cartilage occurs, which in some animals, as the ox, is bony, and is known as the *os cordis*. This central fibro-cartilage is placed in the angle between the aortic and the two auriculo-ventricular openings (see fig. 426), and from it processes pass in various directions. One of these extending downwards to meet the fleshy septum of the ventricles, separates the left ventricle from the right auricle, forming the right boundary of the aortic vestibule. These processes form the bases of what have been described by authors as the *fibrous* or *tendinous rings* of the auriculo-ventricular and arterial openings. The fibrous tissue of these rings is continuous with that which is found in the segments of the valves, strengthened on the sides

next the septum by the processes from the fibro-cartilage. The rings of the arterial orifices give attachment below to some of the muscular fasciculi of the ventricle, whilst above they project between the flaps of the valves, with the curved border of which they are continuous, as well as with the middle coat of the artery. The fibres of the middle coat of the artery, here comparatively thin, are not arranged annularly, as in other parts of the vessel, but converge to the intervals between the sinuses of Valsalva, to be attached to the projections of the fibrous rings.

Fig. 431.

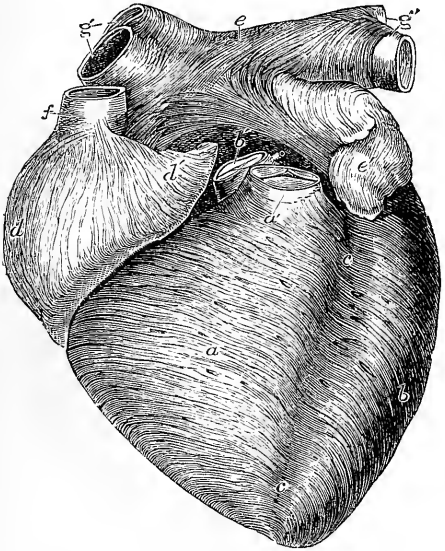


Fig. 431.—Anterior view of heart of a young subject dissected after long boiling, to show the superficial muscular fibres (Allen Thomson). $\frac{2}{3}$

This figure is planned after one of Luschka's, but its details were chiefly taken from an original preparation. The aorta, *b'*, and pulmonary artery, *a'*, have been cut short close to the semilunar valves, so as to show the anterior fibres of the auricles. *a*, superficial layer of the fibres of the right ventricle; *b*, that of the left; *c*, *c*, anterior interventricular groove, from which the coronary vessels have been removed, *d*, right auricle; *d'*, its appendix, both showing chiefly perpendicular fibres; *e*, upper part of the left auricle; between *c*, and *b'*, the transverse fibres which behind the aorta pass across both auricles; *e'*, appendix of left auricle; *f*, superior vena cava, around which, near the auricle, circular fibres are seen; *g*, *g'*, right and left pulmonary veins with circular bands of fibres surrounding them.

The tendinous rings of the aortic and left auricular orifices are confluent, so that when the fibrous tissue is destroyed by boiling the two apertures run into one.

ARRANGEMENT OF THE MUSCULAR FASCICULI.

The arrangement of the fasciculi (or "fibres," as they are ordinarily termed) in the auricles and ventricles must be considered separately, for the muscular bundles of the two are not continuous, being only connected by the fibrous tissue around the auriculo-ventricular orifices: in conformity with this it is seen that, after boiling the heart, the auricles may be easily separated from the ventricles.

Fibres of the auricles.—These consist of a superficial set, common to both cavities, and of deeper fibers proper to each. The *superficial fibres* run transversely over both venous sinuses, and are most numerous on the anterior surface; some pass in at the inter-auricular septum (fig. 431). Of the deeper fibres, which are proper to each auricle, some pass over the auricle, and seem to be attached by both extremities to the corresponding auriculo-ventricular rings (*looped fibres*). Others, which are termed *annular fibres*, encircle the auricular appendages (fig. 431 *d'*, 431 *e'*), some longitudinal fibres running within them. Annular fibres also surround the entrances of the venæ cavæ (*f*, *i*) on the right, and of the coronary vein and the pulmonary veins on the left side of the heart (*g*, *h*),—the muscular fibres extending for some distance from the auricle upon

the veins, especially upon the superior vena cava and the pulmonary veins. The fossa ovalis in the septum is also encircled by annular fibres.

Fibres of the ventricles.—The muscular fasciculi of the ventricles have a very intricate disposition, which has received great attention from anatomists. Many of the statements, however, are conflicting, and it must be confessed that the subject still admits of further investigation.*

The fibres on the outer surface of the ventricles (figs. 431, 432, *a*, *b*) extend from the base, where they are attached to the tendinous structures around the orifices, towards the apex of the heart, where they pass with an abrupt twist into the interior of the left ventricle. Their general direction is not vertical but oblique, especially in front (fig. 431), just as if while the base of the organ remained fixed the apex had been twisted half round in the direction of the motion of the hands of a watch. They form a distinct thin superficial stratum, best marked at the back of the right ventricle, for here the direction of the fibres is quite different from those immediately beneath. At the back they pass over the septum without turning in: at the front they are somewhat interrupted by fibres which come out from the septum; except towards the base and apex, where they cross uninterruptedly from one ventricle to the other (fig. 433).

Fig. 432.

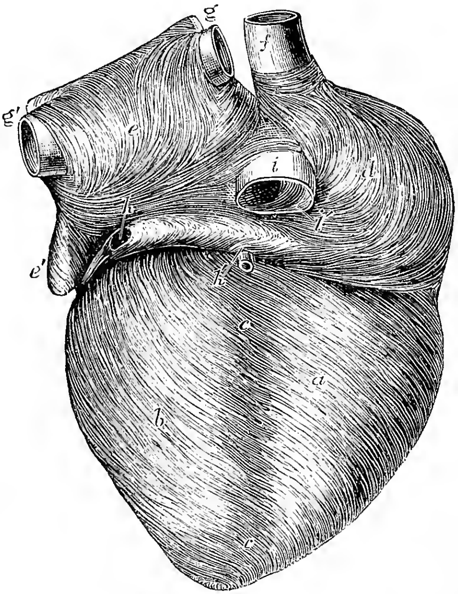


Fig. 432.—Posterior view of the same preparation as is represented in the preceding figure (Allen Thomson). $\frac{2}{3}$

a, right ventricle; *b*, left ventricle; *c*, posterior interventricular groove, from which the coronary vessels have been removed; *d*, right auricle; *e*, the left; *f*, superior vena cava; *g*, *g'*, pulmonary veins cut short; *h*, sinus of the great coronary vein covered by muscular fibres; *h'*, posterior coronary vein joining the principal one; *i*, inferior vena cava; *i'*, Eustachian valve.

If the superficial fibres be traced into the interior of the left ventricle at the apex, it is found that they pass for the most part into continuity with the papillary muscles, and the adjacent parts of the inner layer of muscular fibres of that cavity. Most of those which are seen crossing over the front and left side of the heart can be traced towards the posterior papillary muscles, whilst those which pass over the back and right side of the heart, are chiefly continuous with the anterior papillary muscle. Many of the superficial fibres, however, after gaining the interior of the left ventricle, do not pass into the papillary muscles, but spread out as an inner vertical layer of muscular fasciculi, which pass upwards to be attached to the fibrous rings at the base of the ventricle.

The peculiar spiral concentration of the fibres of the heart at the apex is known as the *vortex* or *whorl*, and is produced, as already described, by the twisting or interlocking of the external fibres as they pass to be continuous with those in

* For convenience of description in the following account of the course of the fibres, the heart is supposed placed apex downwards, and with the anterior and posterior surfaces about equally occupied by the two ventricles (as represented in figs. 431, 432).

the interior. It has been thought that a similar continuity was the rule at the base of the heart also, and that few if any of the bundles are attached to the tendinous rings. But although it is true that some bundles may turn round at the auriculo-ventricular openings, this is by no means general, and most of the muscular fasciculi must be described as being attached to the fibrous and fibro-cartilaginous structures at the base, either directly or through the medium of the chordæ tendineæ and segments of the valves.

Fig. 433.

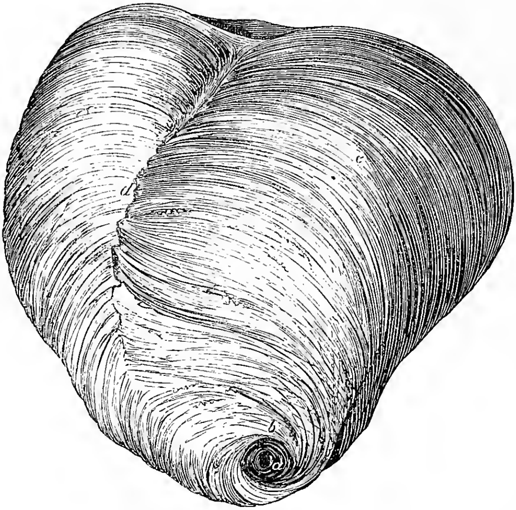


Fig. 433.—Surface fibres of the ventricles of the human heart from the front and below (Reid).

b, bundle of fibres emerging from the interior of the left ventricle at the vortex *a*, and crossing the lower part of the septum uninterruptedly. At *d* the surface fibres are somewhat interrupted.

The greater part of the thickness of the wall of the left ventricle is formed of fibres which are attached above, like those just described, to the fibrous rings at the base. From there they pass obliquely downwards in the posterior and left wall and more directly downwards in the anterior wall towards the apex. But

Fig. 434.

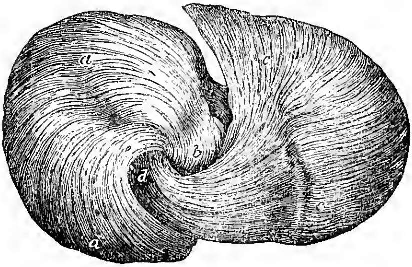


Fig. 434.—View of the fibres of the sheep's heart, dissected at the apex to show the "vortex" (Pettigrew).

a, *a*, fibres entering the apex posteriorly at *b*; *c*, *c*, fibres entering the apex anteriorly at *d*.

before reaching this they are inclined, especially the anterior fibres, somewhat abruptly towards the front of the septum, which they enter near its lower end. They may now be divided into three sets. (1) Many pass at once obliquely upwards in the septum to be attached to the central fibro-cartilage, so that these may be regarded as forming simple V-shaped muscular loops around the cavity of the left ventricle. (2) Others cross in the septum in their passage upwards and pass to the

posterior wall of the right ventricle, being partly continuous with its posterior papillary muscle. (3) Others again pass nearly horizontally into the posterior wall of the left ventricle, and take an annular course in it. But many of these annular fibres of the left ventricle (which are found about the middle of its thickness) are continuous with the deeper fibres of the right ventricle.

The right ventricle so far as regards the arrangement of its muscular fasciculi may be looked upon as an appendage of the left. Its superficial fibres are directly continuous, as we have seen, with the papillary muscles of the left ventricle. Its deeper fibres also mostly pass into continuity with those of the left ventricle. Attached above to the fibrous structure encircling the right auriculo-ventricular and the pulmonary apertures, either directly or (in the case of the papillary muscles) indirectly through the chordæ tendineæ they pass towards the septum. The posterior fibres enter this behind and pass forwards in it to the front of the left ventricle (as above described under 2); the anterior enter the septum in front and pass backwards in it, intercrossing with those just mentioned, to the posterior part of the left ventricle; while the middle set of fibres, derived chiefly from the external wall of the right ventricle, enter the lower part of the septum and are directed upwards in it to be attached to the central fibro-cartilage. Finally a considerable number of fasciculi pass straight across the septum without turning into it and appear to encircle both ventricles. There are besides certain sets of fibres which appear not readily assignable to any of those above described: some, for instance, which encircle the pulmonary orifice, and others which, as Sibson has shown, radiate upwards from the base of the anterior papillary muscle of the right ventricle, to be attached to the tendinous structures at the base of the heart, especially to the pulmonary ring, opposite the two anterior sinuses of Valsalva.

Fig. 435.

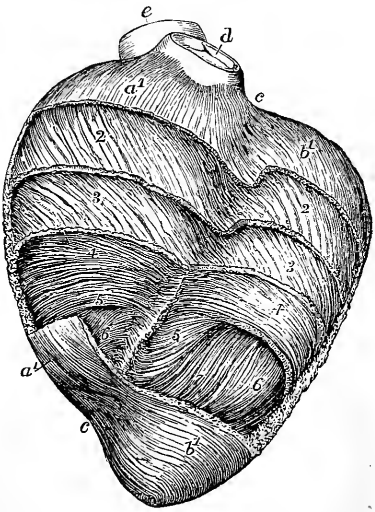


Fig. 435.—View of a partial dissection of the fibres of the anterior wall of the ventricles in a sheep's heart, designed to show the different degrees of obliquity of the fibres (Allen Thomson).

At the base and apex the superficial fibres are displayed: in the intervening space, more and more of the fibres have been removed from above downwards, reaching to a greater depth on the left than on the right side. a^1, a^1, the superficial fibres of the right ventricle; b^1, b^1, the same of the left ventricle; at 2 these fibres have been removed so as to expose those underneath, which are seen to have the same direction as the superficial ones over the left ventricle, but different over the right; at 3 some of these have been removed, but the direction is only slightly different; 4, transverse or annular fibres occupying the middle of the thickness of the ventricular walls; 6, 7, internal fibres passing downwards towards the apex to emerge at the whorl; between *c*, *c*, the anterior coronary or interventricular groove, over which the superficial fibres are seen crossing; in the remaining part of the groove, some of the deeper fibres turn backwards into the septum; *d*, the pulmonary artery; *e*, the aorta.

In the middle of the thickness of the ventricular wall the fibres are, as before said, annular and transverse (fig. 435, 4, 4′); but, as Ludwig showed, they pass by the most gradual transition into the diagonal ones nearer the surfaces, so that any separation into layers which may be effected (with the exception of the

superficial stratum over the right ventricle) must be looked upon as in a great degree artificial.

The muscular fibres of the heart are cross-striated, but differ from the fibres of the voluntary muscles in being constantly branched and united to one another so as to form a complete network or spongework with reticulating interstices. They are moreover composed in the manner already described (pp. 135, 136,) of somewhat oblong occasionally forked cells, cemented together end to end. The interstices between the fibres are filled by connective tissue, with numerous blood-vessels, lymphatics, and nerves.

Vessels.—The muscular substance is supplied with blood by the coronary arteries, the origin and course of which, as well as of the cardiac veins, are elsewhere described. The smaller branches penetrate into every part of the muscular substance, the capillaries being very numerous and closely arranged. The valves are non-vascular, except where muscular tissue occurs in them, as is sometimes found to be the case in the auriculo-ventricular valves (L. Langer).

The lymphatics (which are found in great number beneath both the pericardium and endocardium), are also, as was shown by Schweigger-Seidel, extensively distributed throughout the muscular substance, occurring in the form of freely communicating fissure-like spaces, between the muscular bundles, and lined by epithelioid cells; the mode of origin being thus to a certain extent lacunar. According to Skwartzoff, whose observations were made upon the heart of the rabbit, dog, and calf, the lymphatics of the ventricles are independent of those of the auricles and are chiefly collected into a trunk which lies in the anterior longitudinal groove, turns to the left around the aorta and passing between this vessel and the trachea enters the lymphatic gland or glands which are there situated. From them the lymph passes into the right innominate vein. Other of the cardiac lymphatics pass round at the reflection of the pericardium and over the parietal layer to reach the thoracic duct.

Nerves.—The nerves given off by the cardiac plexuses appear rather small in comparison with the bulk of the heart; they are derived partly from the cerebro-spinal and partly from the sympathetic system (more especially from the pneumogastric nerve, and from the cervical and superior thoracic ganglia of the sympathetic nerve).

Nerves of the auricles. From the cardiac plexuses at the base of the heart, nerves pass to the auricles and there join a plexus chiefly of non-medullated fibres, which is beset with numerous small groups of ganglion-cells. This gangliated plexus lies for the most part immediately beneath the pericardial covering of the auricles, but its branches penetrate into the muscular substance.

In the dog's heart Dogiel found three principal groups of ganglia, viz., one between the superior cava and the right auricular appendix, another between the same vein and the root of the aorta, and a third between the root of the aorta and the pulmonary veins. Schklarewski, in different mammals, describes them as occurring chiefly in the interauricular septum and in the auriculo-ventricular groove. The same is affirmed by Skwartzoff, who, however, found the ganglia on the auricular plexus to be most numerous over the left auricle, and Vignal states, with regard to the human heart, that it is especially near the orifices of the pulmonary veins that they occur in largest number.

Nerves of the ventricles. From the cardiac plexuses at the base

of the heart nerves are given off which, passing downwards along the commencement of the aorta and pulmonary artery, reach the coronary arteries, and accompanying these in their course form secondary plexuses (right and left coronary plexuses) around those vessels. From the coronary plexuses numerous branches proceed, which pass, for the most part, over the surface of the ventricles under the pericardium, but a few small branches are directed upwards to join the auricular plexus of nerves. Small microscopic groups of ganglion-cells occur, as was shown by Remak, both upon the coronary plexuses and also here and there along their branches for a certain distance.

In the frog, the only nerves which pass to the heart are the cardiac branches of the vagi, one from each, which reach the heart along the superior venæ cavæ, and after coursing along the sinus venosus (into the undivided cavity of which the veins pour their blood) enter the septum between the two auricles. In the septum the nerves, now become anterior and posterior, pass down, and at the junction of the auricles with the single ventricle, they each end in a group of ganglion-cells, known as the ganglia of Bidder. But along their whole course in the heart they are beset at intervals with small groups of ganglion-cells, and on all their branches in the venous sinus and in the interauricular septum similar cells occur, either intercalated in the small nervous cords, or set laterally upon them. No ganglion-cells have been proved to occur either on the branches which are distributed to the auricles (with the exception of the septum) or on those which pass to the muscular substance of the ventricle.

The **cardiac pericardium** or **epicardium** has the usual structure of a serous membrane. It is covered externally by a pavement epithelium

Fig. 436.

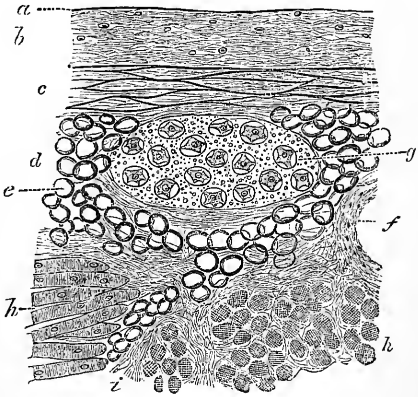


Fig. 436.—Section of a part of the pericardium of the right auricle (E.A.S.).

a, Serous epithelium in section; *b*, connective tissue layer; *c*, elastic network; *d*, subserous areolar tissue; *e*, fat; *f*, section of a blood-vessel; *g*, a small ganglion; *h*, muscular fibres of the myocardium; *i*, intermuscular areolar tissue.

of irregularly polygonal cells and as in other serous membranes stomata are found here and there between these, permitting a communication between the pericardial cavity and the lymphatics of the membrane (Skwartzoff). The substance of the membrane is composed of connective tissue with much elastic tissue, chiefly collected into a well developed network in the deeper layer (fig. 436, *c*).

The subserous areolar tissue is continuous with the interstitial tissue between the fibres of the myocardium. In it run the vessels and nerves before dipping down into the muscular substance, and a system of lymphatic vessels, connected with the lymphatic spaces of the myocardium, also occurs here. The vessels and nerves are generally imbedded in a

considerable amount of fat (fig. 436, *e*), which is especially collected in the furrows, but may in fat subjects extend as a layer covering the greater part of the surface; and may even be found in the larger interspaces of the myocardium, and beneath the endocardium.

The **endocardium** furnishes a lining to all the cavities of the heart, following the inequalities of the inner surface of the organ, and becoming continuous at the venous and arterial orifices with the inner coat of the respective veins and arteries. A layer of flattened epithelial cells covers and lines the inner surface (fig. 437, *a*), and beneath this the endocardium consists of connective tissue with a close network of elastic fibres often passing into fenestrated membrane. Plain muscular fibres are present in some parts (*m*). The ordinary cardiac muscular fibres extend in many places close up to the endocardium, but in others are separated from it by some amount of areolar tissue. In this tissue, fat is often met with, especially in fat subjects and in fatted animals. In the heart of some animals, as the sheep, large beaded reticulating fibres are met with lying in the subendocardial tissue, and, having been first described by Purkinje, are known by his name. When examined with the microscope these fibres of Purkinje are found to be composed of large clear cells, joined end to end, and containing in their centre one or two nuclei (generally two) embedded in a more granular substance. The periphery of the cells in question is composed of transversely striated substance, and they appear to represent a condition of arrested development of cardiac muscular tissue. According to Gegenbaur they are occasionally to be found in the human heart. The endocardium is usually more opaque on the right side than on the left; and thicker in the auricles (the left especially) than in the ventricles; it is, however, very thin on the musculi pectinati of the auricles and on the columnæ carneæ of the ventricles.

Fig. 437.

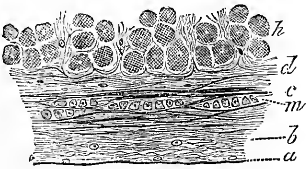


Fig. 437. — SECTION OF A PART OF THE ENDOCARDIUM OF THE RIGHT AURICLE.

a, Lining epithelium; *b*, connective tissue with fine elastic fibres; *c*, layer with coarser elastic fibres; *d*, subendocardial connective tissue continuous with the intermuscular tissue of the myocardium; *h*, muscular fibres of the myocardium; *m*, plain muscular tissue in the endocardium.

DIMENSIONS AND WEIGHT OF THE HEART.

Size.—It was stated by Laennec, as the result of his experience, that the heart in its natural condition is about equal in size to the closed hand of the individual. It is about five inches long, three and a half in its greatest width, and two and a half in its extreme thickness from the sternal to the diaphragmatic surface; but linear measurements of a flaccid organ like the heart must be subject to so many accidental variations as to render them of little value.

Weight.—The weight of the heart in the adult is also subject to considerable variation, ranging between rather wide limits, which depend on the general weight of the body and on the sex.

Its mean weight is about 9 or 10 oz.

According to Reid's tables, the average weight in the adult male is as high as 11 oz., and in the female 9 oz.; while according to Peacock the average of the male is $9\frac{3}{4}$ oz., and that of the female 9 oz. The proportion of the weight of the heart to that of the body is from 1 to 150 to 1 to 170.

It was shown by Clendinning that the heart continued to increase in weight up to an advanced period of life, but at a comparatively slower rate subsequently to the age of twenty-nine years.

Similarly Beneke finds the *volume* of the heart to increase with age, at first rapidly then gradually. Thus in the new-born infant the average volume is 22 cubic centimetres; at the fifteenth year it is 150 cc. to 160 cc.; and at the twentieth year about 250 cc. After this it increases but slowly up to the fiftieth year, by which time it has arrived at 280 cc. Subsequent to this there is a slight gradual diminution. Up to the age of puberty the volume is about the same in both sexes, but after puberty it is 25 cc. to 30 cc. larger in the male. On account of the obvious difficulties of the investigation these statements can however only be regarded as approximate.

The auricles are generally stated to be rather less capacious than the ventricles. The right auricle is also said to be larger than the left, in the proportion of 5 to 4 (Cruveilhier). In the ordinary modes of death, the right ventricle is always found more capacious than the left, probably owing to its being distended with blood: the left ventricle, on the other hand, is found nearly empty, and thus becomes more fully contracted. There are good reasons for believing that during life scarcely any difference of capacity exists between the two cavities.

The right auriculo-ventricular opening, and the orifice of the pulmonary artery, are both found to be somewhat larger after death than the corresponding openings on the left side of the heart.*

Literature.—On the structure of the heart.—*Weismann*, in Arch. f. Anat., 1861; *Eberth*, in Virchow's Archiv, XXXVII.; *Obermaier*, in Arch. f. Anat., 1867; *Lehnert*, in Arch. f. mikr. Anat., 1868; *Schweigger-Seidel*, article "Heart" in Stricker's Handbook, 1871; *Rolleston*, Harveian oration, Brit. Med. Journ., 1873; *Paladino*, Contrib. all'anat. d. cuore, 1876; *Bernays*, in Morph. Jahrb. II. (valves); *Gegenbaur*, in Morph. Jahrb. III. (Purkinje's fibres); *Ranvier*, Leçons faites au Collége de France, 1880; *L. Langer*, in Wiener Sitzungsb., 1880, (on foramina Thebesii and valves).

On the lymphatics of the heart.—*Skwartzoff*, in Pflüger's Archiv, VIII.; *Schumkow*, in the same (lymphatics of pericardium); *Salvioli*, in Arch. p. l. sci. med., 1878.

On the nerves of the mammalian heart.—*Remak*, in Müller's Archiv, 1844; *Skwartzoff*, loc. cit.; *Dogiel*, in Arch. f. mikr. Anat. XIV.; *Schklarewski*, in Göttinger Nachricten, 1872; *Champneys*, in the Journ. of Anat., 1879; *Vignal*, in Arch. de physiol., 1881.

On the dimensions and weight of the heart.—*Reid*, in the Lond. and Edin. Monthly Journal of Med. Science, April, 1843; *T. B. Peacock*, in the same journal, in 1846, and reprinted separately, with additional observations, in 1854; *Clendinning*, in the Medic. Chir. Transact., 1838; *Beneke*, in Marburger Schriften XI., 1879.

On the subject of the arrangement of the cardiac fibres may be consulted *C. F. Wolff*, De ordine fibrarum muscularium cordis; Act. Acad. Petropol. 1780—1792; *C. Ludwig*, in Zeitschrift für rationelle Medizin, 1849; and Müller's Archiv; *Winckler*, in Archiv für Anatomie und Physiologie, 1865; *J. Pettigrew*, in Philosoph. Transactions, 1864; *Sibson*, Medical Anatomy, 1869.

* Tables exhibiting the weight of the heart at different ages, and also the average dimensions of the auriculo-ventricular and arterial orifices, will be found in previous editions of this work.

ORGANS OF RESPIRATION.

Besides the heart, the thorax contains the principal organs of respiration, viz., the lungs and a part of the trachea. The larynx, which is affixed to the upper end of the windpipe, and is not only the entrance for air into the respiratory organs from the pharynx, but also the organ of voice, will be described after the lungs.

THE LUNGS.

The *lungs* occupy by far the larger part of the cavity of the chest, and during life are always in accurate contact with the internal surface of its wall. Each lung is attached at a comparatively small part of its flattened inner or median surface by a part named the *root*. In other directions the lung is free and its surface is closely covered by a serous membrane, which is reflected at the root to the corresponding side of the thorax, and named the (right or left) *pleura*.

THE PLEURÆ.

The **pleuræ** are quite distinct from each other. Each consists of a *visceral* and a *parietal* portion. The visceral portion, *pleura pulmonalis*, covers the lung ; and the parietal portion lines the ribs and intercostal spaces, *pleura costalis*, covers the upper convex surface of the diaphragm, enters into the formation of the mediastinum, and adheres to the sides of the pericardium.

At the root of each lung the visceral and parietal portions of the corresponding pleura are continuous with one another ; and, at the lower border of the root, is a fold of the serous membrane, extending vertically along the inner surface of the lung down to the diaphragm, to which it is attached by its extremity ; this fold is named *ligamentum latum pulmonis*.

Along the inner border of each lung there descends a ligamentous band, an offshoot of the prevertebral fascia, attached above to the bodies of the cervical and first dorsal vertebræ and below to the pericardium and central tendon of the diaphragm. These bands, the "suspensory ligaments of the diaphragm" of Teutleben, embrace the roots of the lungs, and in a measure serve to fix both these and the other parts to which they are attached below.

The upper part of the pleura, together with the apex of the corresponding lung, rises into the root of the neck, reaching from one to two inches above the anterior end of the first rib (half an inch to one and a half inches above the clavicle, Pansch), and passing up under cover of the scaleni muscles. Anteriorly the pleural sacs of opposite sides come nearly or altogether into contact behind the second piece of the sternum, and continue so for some distance ; but opposite the lower end of the sternum the right pleura passes beyond the middle line or remains close to it, while the left recedes to a variable distance. Inferiorly the pleuræ do not pass quite down to the attachments of the diaphragm, but leave a portion of its circumference in contact with the costal parietes. Owing to the height of the diaphragm on the right side (corresponding with the

greater convexity of the liver), the right pleural sac is shorter than the left; it is at the same time wider. Behind, the lower extent of the pleura is as far down as the vertebral end of the twelfth rib, or even in some cases as far as the transverse process of the first lumbar vertebra. In the line of the axilla, the right pleura extends down to the lower edge of the ninth rib, while the left pleura reaches to the lower edge of the tenth (Luschka). In front the right pleura reaches down to the junction of the seventh rib with its cartilage; the left pleura a little lower.

A small slip of muscle arising from the transverse process of the last cervical vertebra, is described by Sibson as expanding into a dome-like aponeurosis or fascia, which covers or strengthens the pleural cul-de-sac, and is attached to the whole of the inner edge of the first rib.

Structure.—The pleura possesses the usual characters of serous membranes. The costal part is the thicker, and may be easily raised from the ribs and intercostal spaces. It is strengthened here by a layer of subserous areolar tissue of considerable thickness. On the pericardium and diaphragm the pleura is thinner and more firmly adherent; but it is thinnest and least easily detached upon the surface of the lungs. A difference is also noticeable in the character of the superficial epithelial layers, for while on the *pleura costalis* this consists of the ordinary flattened cells, on the *pleura pulmonalis* the cells are less distinctly flattened and more granular and polyhedral, but they become flattened out when the lung is distended (Klein). Lymphatic vessels are abundant in and beneath the pleura as in other serous membranes, and they communicate in many parts, by means of stomata, with the cavity of the membrane. In the *pleura costalis* the stomata are only found over the intercostal spaces not over the ribs (Dybkowsky).

Beneath the serous covering there is placed a thin layer of *subserous* areolar tissue mixed with a large number of elastic fibres. It is continuous with the areolar tissue in the interior of the lung, and has been described as a distinct coat under the name of the second or deeper layer of the pleura. In the lungs of many animals, such as the lion, seal, and leopard, this subserous layer forms a very strong membrane, composed principally of elastic tissue; in others, as the guinea-pig, a network of plain muscular fibres is found which have a general radiating direction from the apex (Klein). A close plexus of lymphatic vessels is also met with in this sub-pleural tissue: these vessels communicate on the one side by means of stomata with the pleural cavity, and on the other, as will be afterwards noticed, with a network of similar vessels in the inter-alveolar septa of the lungs. A uniform network of capillary blood-vessels covers the surface of the lung. These are supplied from branches of the bronchial arteries. They are less closely arranged than the blood-vessels of the pulmonary alveoli, and are thus as well as by their position easily distinguishable from them in specimens of injected lung.

THE LUNGS.

Each lung is irregularly pyramidal or conical, with the base downwards (fig. 438). The broad, concave *base* is of a semilunar form, and rests upon the arch of the diaphragm. It is bounded by a thin margin,

which is received in the angle between the ribs and the diaphragm, and reaches much lower down behind and at the outer side than in front. The *apex* is blunt, and, as already mentioned, reaches into the root of the neck, above the first rib, where it is separated from the first portion of the subclavian artery by the pleural membrane. The apex is generally marked by a groove where the subclavian artery crosses it. The *outer surface*, which moves upon the thoracic parietes, is smooth, convex, and of great extent, corresponding with the arches of the ribs and costal cartilages. The *inner surface* is concave, and in part adapted to the convex pericardium. The *posterior* border is rounded, and is received into the deep groove formed by the ribs at the side of the vertebral column ; measured from above downwards, it is the longest part of the lung. The *anterior* border is thin and overlaps the pericardium, forming a sharp edge, which, opposite the middle of the sternum, is separated during inspiration from the corresponding margin of the opposite lung only by the two thin layers of the mediastinal septum. Upon the inner surface, somewhat above the middle of the lung, and considerably nearer

Fig. 438.

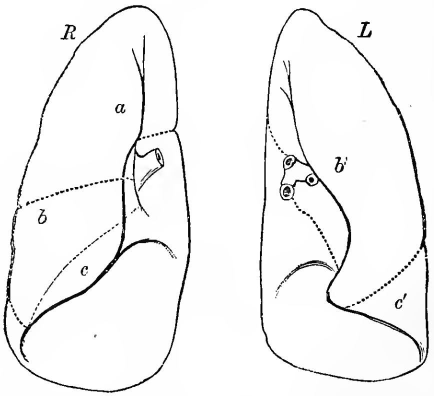


Fig. 438.—Outline of the lungs from before (after His). ¼

R, right lung ; *L*, left lung ; *a*, *b*, *c*, upper, middle, and lower lobe of right lung; *b'*, *c'*, upper and lower lobes of left lung. The fissures are indicated by dotted lines.

to the posterior than the anterior border, is the *root*, where the bronchi and great vessels join the lung.

The left lung is divided into two lobes by a long and deep *fissure*, which penetrates obliquely upwards and inwards from the outer surface to within a short distance of the root. The *upper lobe* is the smaller, and is irregularly conical, with an oblique base and rounded apex, whilst the *lower* is quadrilateral. In the right lung there are two fissures, which pass the one from above the middle of the external surface, and the other from near its lower end, and converge towards the root, thus marking off three lobes, an *upper*, *middle*, and *lower*. Of the two fissures, the upper is less extensive than the lower, and in consequence, the middle

lobe, which is usually much smaller than the others, appears at first sight to be more closely connected with the upper lobe, and is usually described as forming a part of it.

In spite, however, of its comparatively small size, it appears not improbable, from the researches of Aeby, which will be afterwards more fully referred to, that the middle lobe of the right lung is the morphological equivalent of the whole upper lobe of the left lung.

The left lung has a deep notch in its anterior border, into which the apex of the heart (enclosed in the pericardium) is received. Besides these differences the right lung is shorter than the left, owing to the diaphragm rising higher on the right side to accommodate the liver, whilst the left lung is the narrower, owing to the heart and pericardium encroaching on the left half of the thorax. On the whole, however, as is seen on a comparison of their weights, the right is the larger of the two lungs.

At the summits and posterior borders the extent of the lungs corresponds with that of the pleural sacs which contain them, but in front and below the relation is variable, inasmuch as the anterior margins pass forwards most completely between the mediastinal and costal pleuræ during inspiration, and retire to a variable degree from between them in expiration ; and in like manner the inferior margins descend, during inspiration, between the costal and diaphragmatic pleuræ ; probably at no time do they ever descend completely to the line of reflection between those membranes.

The root of each lung is composed of the bronchus or sub-division of the air-tube, and the large blood-vessels, together with nerves, lymphatic vessels, and glands, connected together by areolar tissue, and enclosed by the reflection of the pleura.

The root of the right lung lies behind the superior vena cava and part of the right auricle, and below the azygos vein, which arches over it to enter the superior cava. That of the left lung passes below the arch of the aorta, and in front of the descending aorta. The phrenic nerve descends in front of the root of each lung, and the pneumogastric nerve behind, whilst the ligamentum latum pulmonis is continued from the lower border. The bronchus, together with the bronchial arteries and veins, the lymphatics and lymphatic glands, are placed on a plane posterior to the great blood-vessels, whilst the pulmonary veins are in front of the arteries. The pulmonary plexuses of nerves lie on the anterior and posterior aspect of the root, beneath the pleura, the posterior plexus being the larger of the two.

On the right side the undivided portion of the bronchus is altogether above the right pulmonary artery, on the left side the undivided portion of the bronchus, which is considerably longer than on the right side, extends to below the level of the left pulmonary artery which crosses it. On both sides the pulmonary veins are below the corresponding arteries.

Before entering the substance of the lung, the right bronchus gives off the branch to the upper lobe, and is then continued on into the lower lobe, the branch for the middle lobe being given off from the continuation. The corresponding branch of the left bronchus is considerably larger, and enters the upper lobe of its lung. The main branches of the

pulmonary vessels are distributed like the bronchi. Within the lung the arterial trunks run behind the bronchial branches, the venous trunks in front.

Dimensions of the lungs.—The lungs vary much in size and weight according to the quantity of blood they may happen to contain, as well as from other causes. The weight of both lungs together, as generally stated, ranges from 30 to 48 ounces, the more prevalent weights being found between 36 and 42 ounces. The proportion borne by the right lung to the left is nearly that of 22 ounces to 20, taking the combined weight of the two at 42 ounces. The lungs are not only absolutely heavier in the male than in the female, but appear to be heavier in proportion to the weight of the body.

According to the observations of Reid the average weight in 29 males was found to be 24 oz. for the right lung, and 21 oz. for the left; and in 21 females, 17 oz. for the right, and 15 oz. for the left lung.

Physical properties.—The substance of the lung is of a light porous spongy texture, and, when healthy, is buoyant in water: but in the fœtus, before respiration has taken place, and also in certain cases of congestion, collapse, or consolidation from disease, the entire lungs, or portions of them, sink in that fluid. The specific gravity of a healthy lung, as found after death, varies from 0·345 to 0·746. When the lung is fully distended its specific gravity is 0·126, whilst that of the pulmonary substance, entirely deprived of air, is 1·056 (Krause). When pressed between the fingers, the lungs impart a crepitant sensation, which is accompanied by a peculiar noise, both effects being caused by the air contained in the tissue. On cutting into the lung, the same crepitation is heard, and there exudes from the cut surface a reddish frothy fluid, which is partly mucus from the air-tubes and air-cells, and partly serum of blood, rendered frothy by the admixed air.

The pulmonary tissue is endowed with great elasticity, in consequence of which the lungs collapse to about one-third of their bulk when the thorax is opened. Owing to this elasticity also, the lungs, if artificially inflated out of the body, contract to their previous volume when the air is again allowed to escape.

In infancy the lungs are of a pale rose-pink colour, which might be compared to blood-froth; but as life advances they become darker and are mottled or variegated with spots, patches, and streaks of dark slate-colour, which sometimes increase to such a degree as to render the surface almost uniformly black.

The dark colouring matter found in these streaks is in the form of granules and collections of granules, frequently not inclosed in cells; it is deposited in the interstitial areolar tissue mostly near the surface of the lung, and is not found so abundantly in the deeper substance. It exists sometimes in the air-cells, and on the coats of the larger vessels. Its quantity increases with age, and is said to be less abundant in females than in males. In persons who follow the occupation of miners, more especially colliers, the lungs are often intensely charged with black matter. The black substance seems mainly to consist of particles of carbonaceous substance. It is found also in the bronchial glands; indeed, it appears to be taken up in large measure by the lymphatics. In exceptional cases the adult lungs exhibit only very slight streaks of pigment.

Condition in the fœtus and changes after birth.—In the fœtus the lungs contain no air, and consequently sink in water. They undergo very rapid and remarkable changes after birth, in consequence of the commencement of respiration: these affect their size, position, form, consistence, texture, colour, and weight, and should be carefully studied, as furnishing the only means of distinguishing between a still-born child and one that has respired.

1. *Position, size, and form.*—In a fœtus at the full period, or in a still-born child, the lungs, comparatively small, lie packed at the back of the thorax, and do not entirely cover the sides of the pericardium; subsequently to respiration, they expand, and completely cover the pleural portions of that sac, and are also in contact with almost the whole extent of the thoracic wall, where it is covered with the pleural membrane. At the same time, their previously thin sharp margins become more obtuse, and their whole form is less compressed.

2. *Consistence, texture, and colour.*—The introduction of air and of an increased quantity of blood into the fœtal lungs, which ensues immediately upon birth, converts their tissue from a compact, heavy, granular, yellowish-pink, gland-like substance, into a loose, light, rose-pink, spongy structure, which, as already mentioned, floats in water. The changes thus simultaneously produced in their consistence, colour, and texture, occur first at their anterior borders, and proceed backwards through the lungs: they, moreover, appear in the right lung a little sooner than in the left.

3. *Weight.*—The *absolute weight* of the lungs having gradually increased from the earliest period of development to birth, undergoes at that time, from the quantity of blood then poured into them, a very marked addition, amounting to more than one third of their previous weight: for example, the lungs before birth weigh about one and a half ounce, but after complete expansion by respiration, they weigh as much as two and a half ounces. The *relative weight* of the lungs to the body, which at the termination of intra-uterine life is about 1 to 70, becomes, after respiration, on an average, about 1 to 35 or 40; a proportion which is not materially altered through life. The *specific gravity* is at the same time changed from 1·056 to about ·342.

THE TRACHEA AND BRONCHI.

The **trachea** or **windpipe** (fig. 439, *tr.*), the common air-passage of both lungs, is an open tube which commences above at the larynx, and divides below into two smaller tubes, right and left bronchi, one for each lung.

The trachea is placed in the median plane of the body, and extends from the lower border of the cricoid cartilage of the larynx (*c*), on a level with the 6th cervical vertebra in the neck, to a place opposite the disk between the 4th and 5th dorsal vertebræ in the thorax, where it is crossed in front by the arch of the aorta, and at or immediately below that point bifurcates into the two bronchi. It usually measures from four inches to four inches and a half (10 to 11 centimeters) in length, and from three-quarters of an inch to one inch (2 to 2½ centim.) in width; but its length and width are liable to much variation, according to the position of the larynx and the direction of the neck; moreover, it gradually increases in calibre from above downwards (Aeby). Its average diameter is greater in the male than in the female. In front and at the sides the trachea is rendered cylindrical, firm, and resistant, by a series of cartilaginous rings; these, however, are deficient behind,

so that the posterior portion is flattened and entirely membranous (fig. 440). Near its bifurcation the trachea is somewhat expanded laterally.

In the fœtus the trachea is flattened before and behind, its anterior surface being even somewhat depressed ; the ends of the cartilages touch ; and the sides of the tube, which now contains only mucus, are applied to one another. The effect of respiration is at first to render the trachea open, but it still remains somewhat flattened in front, and only later becomes convex.

Relations of the trachea to neighbouring parts.—The windpipe is nearly everywhere invested by a loose areolar tissue, abounding in elastic

Fig. 439.

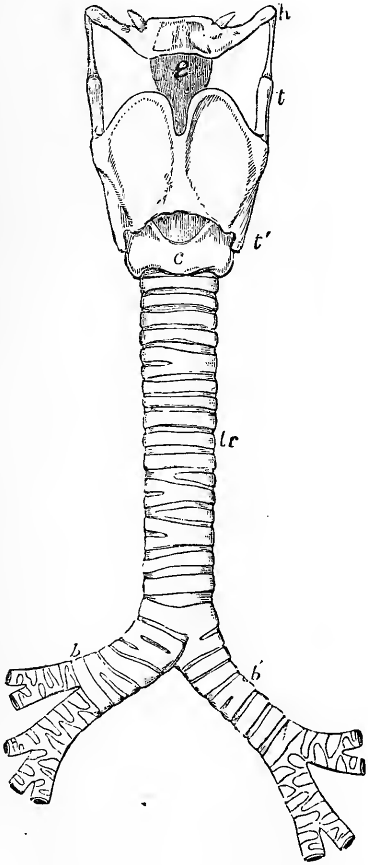


Fig. 439.—Outline showing the general form of the larynx, trachea, and bronchi, as seen from before (Allen Thomson). $\frac{1}{3}$

h, the great cornu of the hyoid bone; *e*, epiglottis ; *t*, superior, and *t'*, inferior cornu of the thyroid cartilage ; *c*, middle of the cricoid cartilage ; *t r*, the trachea, showing sixteen cartilaginous rings ; *b*, the right, and *b'*, the left bronchus. In this and also in the succeeding figure the right bronchus is represented too nearly horizontal (see p. 510 and fig. 441).

fibres, and is very moveable on the surrounding parts. Both in the neck and thorax, it rests behind against the gullet, which intervenes between it and the vertebral column, but towards its lower part projects somewhat to the left side. The recurrent laryngeal nerves ascend to the larynx on each side in the angle between these two tubes.

In the neck the trachea is situated between the common carotid arteries ; at its upper end it is embraced by the lateral lobes of the thyroid body, the middle part or isthmus of which lies across it just below the larynx. It is covered in front by the sterno-thyroid and sterno-hyoid muscles, between which, however, there is left an elongated lozenge-shaped interval in the middle line : this interval is covered in by a strong process of the deep cervical fascia, while, more superficially, another layer not so strong crosses between the sterno-mastoid muscles. The inferior thyroid veins and the *arteria thyroidea ima,* when that vessel exists, also lie upon its

anterior surface; whilst at the root of the neck, in the episternal notch, the innominate artery and the left carotid pass obliquely over it as they ascend to gain its sides.

In the thorax, the trachea is covered by the manubrium sterni, together with the sterno-thyroid and sterno-hyoid muscles; lower down, by the left innominate vein, then by the commencement of the innominate artery and left carotid, which pass round to its sides; and lastly by the arch of the aorta and the deep cardiac plexus of nerves. Placed between the two pleuræ, the trachea is contained in the superior mediastinum, and has on its right side the pleura and pneumogastric nerve, and on the left, the left carotid artery, the pneumo-gastric and its recurrent branch, together with some cardiac nerves.

Fig. 440.

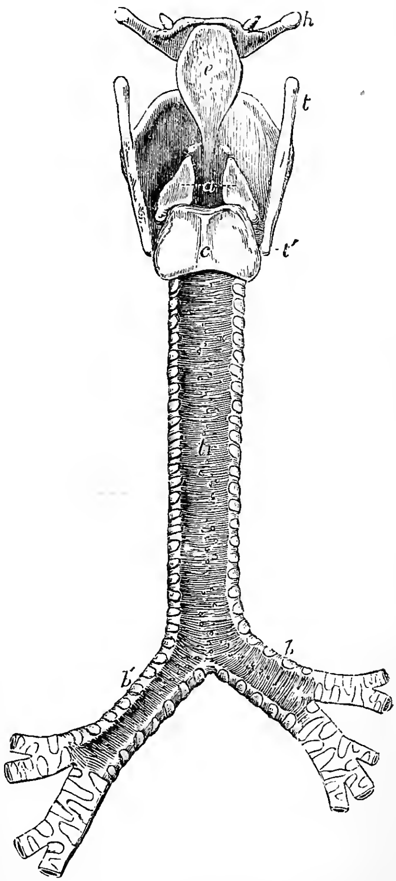


Fig. 440.—Outline showing the general form of the larynx, trachea, and bronchi, as seen from behind (Allen Thomson). ½

h, great cornu of the hyoid bone; *t*, superior, and *t′*, inferior cornu of the thyroid cartilage; *e*, the epiglottis; *a*, points to the back of both the arytenoid cartilages, which are surmounted by the cornicula; *c*, the middle ridge on the back of the cricoid cartilage; *t r*, the posterior membranous part of the trachea; *b*, *b′*, right and left bronchi.

The **right and left bronchi** (figs. 439, 440, *b*, *b′*) proceed each to the root of the corresponding lung, and then undergo division. Previous to this they exactly resemble the trachea on a smaller scale; being rounded and firm in front and at the sides, where they are provided with imperfect cartilaginous rings, and flattened and membranous behind. The undivided portion of the right bronchus (*b*), wider but shorter than the left, measuring about an inch ($2\frac{1}{2}$ centim.) in length, passes obliquely downwards and outwards into the root of the right lung: it is embraced above by the vena azygos, which hooks forwards over it, to end in the vena cava superior; the right pulmonary artery lies at first below it and then in front of it. On looking down the windpipe towards the bifurcation, the right bronchus appears to be a more direct continuation of the trachea than the left. The undivided portion of the left bronchus (*b′*), smaller in

diameter, but longer than the right, being nearly two inches (5 centim.) in length, inclines downwards and outwards beneath the arch of the aorta to reach the root of the left lung. Its termination is about an inch lower than that of the right bronchus. The left bronchus crosses over the front of the gullet and descending aorta: the arch of the aorta turns backwards and to the left over it, and the left pulmonary

Fig. 441.

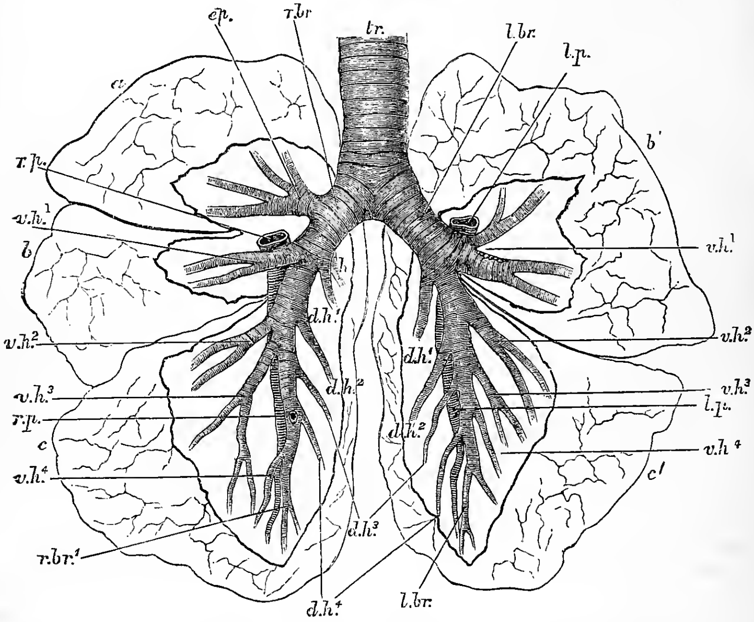


Fig. 441.—Sketch showing the lower end of the trachea, its division into the two bronchial trunks, and the course and chief branches of these within the lungs, from before (after Aeby).

a, upper; *b*, middle; *c*, lower lobe of the right lung; *b′*, upper; *c′*, lower lobe of the left lung; *r.p.* right pulmonary artery; *l.p.* left artery; *r.br.* right bronchial trunk; *l.br.* left bronchial trunk; *ep*, on the right side, eparterial branch supplying the upper lobe; $v.h.^1$, first ventral hyparterial bronchus supplying the middle lobe on the right side, the upper lobe on the left; $v.h.^2$, $v.h.^3$, $v.h.^4$, the remaining ventral hyparterial branches distributed in the lower lobe on each side; $d.h.^1$, $d.h^2$, $d.h.^3$, $d.h.^4$, the four dorsal hyparterial branches distributed on both sides in the posterior and inner part of the lower lobe; *h*, accessory bronchus arising close to the first dorsal hyparterial bronchus on the right side, and representing the one which supplies the azygos lobule in some animals.

artery lies first above it and then on its anterior surface. The relative position of each bronchus in the root of the corresponding lung has been already described.

The right bronchus is generally said to have a more horizontal direction than the left. According to Aeby this is however not the case, the right bronchus being the more oblique. The undivided part of the right bronchus is the shorter in consequence of the fact that this bronchus soon gives off a branch to be dis-

tributed in the upper lobe of the lung (Fig. 441, *ep*). This branch, which comes off *above* the place where the right pulmonary artery crosses the bronchus (eparterial branch), is not represented on the left side in man, and it is hence inferred by Aeby that the lobe of the lung to which it is distributed is also absent on the left side, and that the upper lobe of the left lung is in reality the homologue of the middle lobe of the right lung. All the other branches of the right bronchus, and all the branches of the left bronchus, come off below the place where the corresponding pulmonary artery crosses the air-tube (hyparterial).

In many animals the bronchi, instead of dividing, as in man they appear to do, into nearly equal branches at the root of the lung, pass down in the form of main trunks towards the extremity of the lower lobe, giving off branches at regular intervals in two directions, viz., dorsally and ventrally. The character of the ramification of the (hyparterial) bronchial trunk as it is continued in the lung is therefore bipinnate and not dichotomous. In addition to these two rows of dorsal and ventral branches, accessory branches are occasionally met with coming off from the main trunk in its passage through the lower lobe. These generally arise from the front and are intermediate in position between the dorsal and ventral series, generally taking origin near one or other of these. Of the accessory bronchi the only one that claims especial notice is one which arises near the first dorsal branch of the right bronchial trunk, and which in some animals (monkeys) supplies a special small lobe placed mesially behind the pericardium and termed by Owen the azygos lobe. In some animals well-developed eparterial branches arise from *both* bronchi and supply corresponding lobes in the two lungs. In some (sheep, ox), the eparterial bronchus to the right upper lobe springs directly from the trachea; and a similar condition has in rare cases been met with in the human subject.

In the human lung the same character of bronchial ramification can be made out (fig. 441). From the continuation of the bronchus four dorsal and as many ventral hyparterial branches are given off in succession in each lung. Of these the ventral or outer are much the larger, and the first ventral branch supplies the middle lobe of the right and the upper lobe of the left lung. But the subordination of the branches to the trunk becomes obscured in consequence of the size of the ventral branches, which are as large in most cases as the trunk itself; the latter can nevertheless be detected pursuing with but little deviation a course towards the posterior and lower extremity of the inferior lobe.

On the whole there is a gradual increase in the combined sectional area of the system of air-tubes in proceeding from the commencement of the trachea to the terminations of the bronchial tubes in the lungs; the increase being only interrupted at one point, namely, immediately below the origin of the first branches which are given off from the bronchial trunks. The combined sectional area is here no greater than the sectional area at the lower end of the trachea, although the combined area of the undivided bronchi is distinctly greater than this. (C. Aeby, Der Bronchialbaum der Säugethiere und des Menschen, Leipzig, 1880.)

STRUCTURE OF THE AIR-TUBES.

TRACHEA.—The trachea consists of an elastic framework of incomplete cartilaginous rings or hoops united by fibrous tissue, and at one part by plain muscular tissue. It is lined throughout by a mucous membrane, and provided with glands.

The **cartilages** are from sixteen to twenty in number. Each presents a curve of rather more than two-thirds of a circle, resembling the letter C. The depth from above downwards is three or four millimeters, and the thickness 1 mm. The outer surface of each is flat, but the inner is convex from above downwards, so as to give greater thickness in the middle than at the upper and lower edge. The cartilages are held

together by a strong fibrous membrane, which is elastic and yielding to a certain extent, and not only occupies the intervals between them, but is prolonged over their outer and inner surfaces, so that they are, as it were, imbedded in the membrane.

The cartilages terminate abruptly behind by rounded ends, but the

Fig. 442.

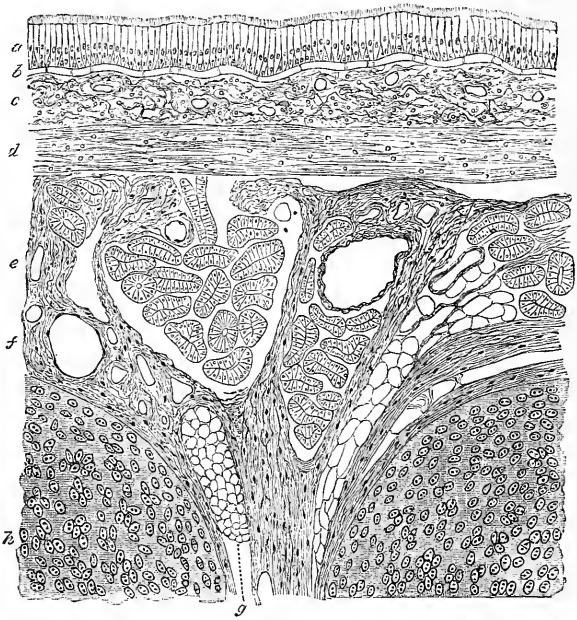


Fig. 442.—Longitudinal section of the human trachea, including portions of two cartilaginous rings (Klein and Noble Smith). Moderately magnified.

a, ciliated epithelium ; *b*, basement membrane ; *c*, superficial part of the mucous membrane, containing the sections of numerous capillary blood-vessels and much lymphoid tissue ; *d*, deeper part of the mucous membrane, consisting mainly of elastic fibres ; *e*, submucous areolar tissue, containing the larger blood-vessels, small mucous glands (their ducts and alveoli are seen in section), fat, &c., ; *f*, fibrous tissue investing and uniting the cartilages ; *g*, a small mass of adipose tissue in the fibrous layer ; *h*, cartilage.

fibrous membrane is continued across between them, and completes the tube behind ; it is here looser in its texture.

The first or highest cartilage, which is connected by the fibrous membrane with the cricoid cartilage of the larynx, is broader than the rest, and often divided at one end. Sometimes it coalesces to a greater or less extent with the cricoid or with the one below. The lowest cartilage, placed at the bifurcation of the trachea, is peculiar in shape ; its lower border being prolonged downwards, and at the same time bent backwards so as to form a curved projection between the two bronchi. The cartilage next above this is slightly widened in the middle line. Sometimes the extremities of two adjacent cartilages are united, and not unfrequently a cartilage is divided at one end into two short branches, the opposite end of that next it being likewise bifurcated so as to maintain the parallelism of the entire

series. The use of these cartilaginous hoops is to keep the windpipe open, a condition essential for the free passage of air into the lungs.

Within the fibrous membrane at the posterior flattened part of the trachea, is a continuous pale reddish layer of *unstriped muscular fibres*, which pass across, not only between the ends of the cartilages, but also opposite the intervals; they doubtless serve to narrow the tube by approximating the ends of the cartilages. Those opposite the hoops are attached to the extremities of the latter, and encroach also for a short distance upon their inner surface. Outside the transverse fibres are a few fasciculi having a longitudinal direction.

Fig. 443.

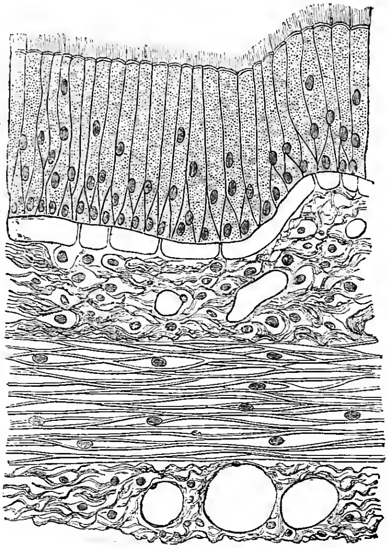


Fig. 443.—A PART OF THE SECTION REPRESENTED IN THE PRECEDING FIGURE MORE HIGHLY MAGNIFIED (Klein and Noble Smith).

The letters represent the same parts as in that figure.

The submucous tissue consists of loose areolar tissue which serves to connect the mucous membrane with the fibrous layer and the cartilaginous rings. It contains mucous glands and a quantity of adipose tissue is often found in it.

The **mucous membrane** (fig. 443, *c*) is smooth and of a pale pinkish white colour in health, although when congested or inflamed, it becomes intensely purple or crimson. It contains a considerable amount of lymphoid tissue. Underneath the epithelium is a basement membrane (fig. 443, *b*), well marked in the human trachea, through which processes from the subjacent connective tissue cells and cell-spaces here and there pass into the epithelium. Throughout the mucous membrane a number of fine elastic fibres are found, but in the deeper parts the elastic fibres are very large and numerous (*d*). Along the posterior membranous part, they are more abundant than elsewhere, and are there collected into distinct longitudinal bundles, which produce visible elevations or flutings of the mucous membrane. These bundles are particularly strong and numerous opposite the bifurcation of the trachea.

The epithelium consists of a layer of columnar ciliated cells, often very irregular at their fixed end, where they are impressed by smaller cells, between which they penetrate to reach the basement membrane. The cilia serve to drive the mucous secretion upwards towards the larynx. Between these ciliated cells, are found others, some rounded others elongated; the latter being prolonged at one end towards the surface, whilst the other end, which is not unfrequently forked, reaches to the subjacent membrane. A few lymph corpuscles are also found

amongst the epithelial cells, as in other epithelia. Some of the cells secrete mucus, and hence goblet-cells are frequently found here (see p. 44).

The trachea is provided with numerous small *mucous glands*. The largest are situated at the back part of the tube, either close upon the outer surface of the fibrous layer, or occupying little recesses formed between its meshes. Smaller glands are found between the cartilaginous rings, upon and within the fibrous membrane, and still smaller ones close beneath the mucous membrane. They are compound glands, and their cavities are lined by a columnar or cubical epithelium : the excretory ducts pass through the muscular layer and the mucous membrane, on the surface of which their orifices are perceptible.

Vessels and Nerves.—The *arteries* of the trachea are principally derived from the inferior thyroid. The larger branches run for some distance longitudinally, and then join a superficial capillary plexus with polyhedral meshes. The *veins* enter the adjacent plexuses of the thyroid veins. A rich plexus of *lymphatics* may readily be injected in the mucous membrane and submucous tissue, but the lymphoid follicles, so common in the alimentary mucous membrane, and also in the walls of the smaller bronchi, are rarely present. When found it is generally surrounding the ducts of the glands as they pass through the mucous membrane The *nerves* come from the trunk and recurrent branches of the pneumo-gastric, and from the sympathetic system. There are said to be numerous ganglia upon them, especially outside the muscular layer at the back of the tube. Their mode of termination has not yet been satisfactorily traced.

In the dog, cat, sheep, and rabbit, the upper half of the trachea is said to be supplied chiefly by the superior laryngeal nerve, through the anastomosis between the superior and inferior nerves in the larynx (Kandarazi).

Bronchi.—The general structure of the undivided portions of the bronchi corresponds with that of the trachea in every particular. Their cartilaginous rings, which resemble those of the trachea in being imperfect behind, are, however, shorter and narrower. The number of these rings on the right side varies from six to eight, whilst on the left the number is from nine to twelve.

The bronchi are supplied by the bronchial arteries and veins, and the nerves are from the same source as those of the lower part of the trachea.

Termination of the bronchi; structure of the bronchial tubes. The principal divisions of the bronchi, as they pass into the lungs, divide into tubes of less calibre, and these again subdivide in succession into smaller and smaller tubes, often distinguished as *bronchia*, *bronchioles*, or *bronchial tubes*, which, diverging in all directions, never anastomose, but terminate separately. The larger branches diverge at acute angles, but the more remote and smaller ramifications spring less acutely. After a certain stage of subdivision each bronchial tube, reduced to a small size (about 1 mm.), is termed a *lobular* or *respiratory bronchial tube* (Kölliker), and its walls become beset with small hemispherical saccules, termed *air-cells*, or *alveoli*. They occur at first only here and there and confined to one side of the tube only, but at length almost cover it so that the tube in great measure loses its cylindrical character. At length it ends in an enlarged completely sacculated passage termed the *alveolar passage*, from which are given off blind ramifications,

somewhat enlarged towards their extremities, and everywhere closely beset with the air-cells. These enlarged terminations are named *infundibula* (fig. 446).

Fig. 444.

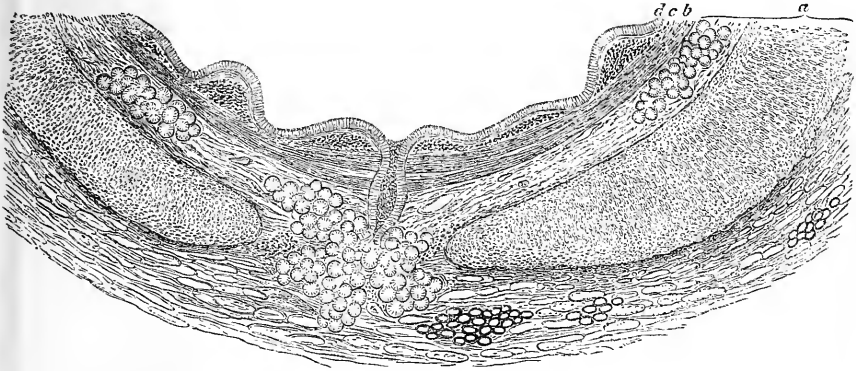


Fig. 444.—Portion of a transverse section of a bronchial tube, human (6 mm. in diameter) (F. E. Schultze). Magnified 30 diameters.

a, cartilage and fibrous layer with mucous glands, and, in the outer part, a little fat; in the middle, the duct of a gland opens on the inner surface of the tube; *b*, annular layer of involuntary muscular fibres; *c*, elastic layer, the elastic fibres in bundles which are seen cut across; *d*, columnar ciliated epithelium.

Within the lungs the air-tubes are not flattened behind like the bronchi and trachea, but form completely cylindrical tubes. Hence, although

Fig. 445.

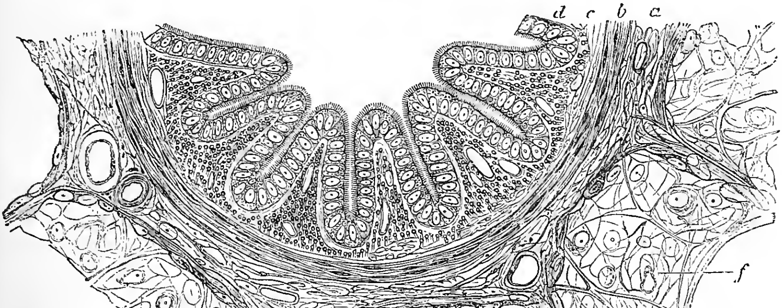


Fig. 445.—Section of a small bronchial tube (4 mm. in diameter) from the pig's lung (F. E. Schultze). Magnified 240 diameters.

a, fibrous layer; *b*, muscular layer; *c*, mucous membrane in longitudinal folds, with numerous longitudinally running elastic fibres cut across; *d*, ciliated epithelium; *f*, surrounding alveoli.

they contain the same elements as the larger air-passages, they are reduced gradually to a state of greater tenuity, but possess certain peculiarities of structure. Thus, the *cartilages* no longer appear as imperfect rings running only upon the front and lateral surfaces of the air-tube, but are disposed over all sides of the tubes in the form of irregularly shaped plates and incomplete rings of various sizes. These are most developed at the points of division of the bronchia, where they form a sharp concave ridge projecting inwards into the tube. They may be traced, becoming rarer and rarer and more reduced in size, as far as bronchia one millimeter in diameter. The *fibrous* coat extends to the smallest tubes, becoming thinner by degrees and degenerating into areolar tissue. In

Fig. 446.

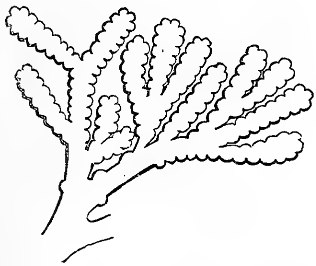


Fig. 446.—Diagrammatic representation of the termination of a bronchial tube in a group of infundibula. (E.A.S.)

it are mucous glands which send their ducts to open on the mucous membrane. These occur most numerously in the larger tubes; in those which measure less than 1 mm. they are rarely if ever found. The *mucous membrane,* which extends throughout the whole system of air passages, is also thinner than in the trachea and bronchus, but it retains its ciliated columnar epithelium (figs. 444, 445, *d*). The longitudinal bundles of *elastic* fibres (*c*, in the transverse sections) are very distinct in both the large and small bronchia, and may be followed by dissection as far as the tube can be laid open, and by the microscope into the smallest tubes. The *muscular* fibres, which in the trachea and bronchi are confined to the back part of the tube, surround the bronchial tubes with a continuous layer of annular fibres, lying inside the cartilaginous plates (*b*); they are found, however, beyond the place where the cartilages cease to exist, and appear as irregular annular fasciculi even in the smallest tubes.

STRUCTURE OF THE PULMONARY PARENCHYMA.

At the point where the small bronchial tubes lose their cylindrical character, and begin to be beset with air-cells, their structure also gradually undergoes a change. The muscular layer almost disappears, the longitudinal elastic bundles are broken up into an interlacement of areolar and elastic tissue, which surrounds the mouths of the air-cells and the walls of the infundibula, and the columnar ciliated epithelium gives place to a stratum of non-ciliated cells. The change in the character of the epithelium first occurs in the so-called respiratory bronchioles, where patches of small pavement epithelium-cells begin to appear amongst the ciliated cells, especially in the neighbourhood of the air-cells upon the wall of these tubes. At the end of the respiratory bronchiole, near the passage to the infundibula, all the cells which line the wall of the tube are of the non-ciliated pavement variety. But the air-cells themselves, both those which are scattered over the respiratory bronchioles and those which cover the infundibula, as well as intermediate portions of the infundibula which occur here and there between the

air-cells, possess an epithelium of a peculiar character. The cells of this epithelium are of two kinds, viz. :—1, large, thin, very delicate cells, irregular in size and shape, lying over the blood-vessels, but also in many cases extending over the interstices between them; they appear not to possess a nucleus: and, 2, small, flat, polygonal, nucleated cells, which lie singly or in small groups of two or three

Fig. 447.

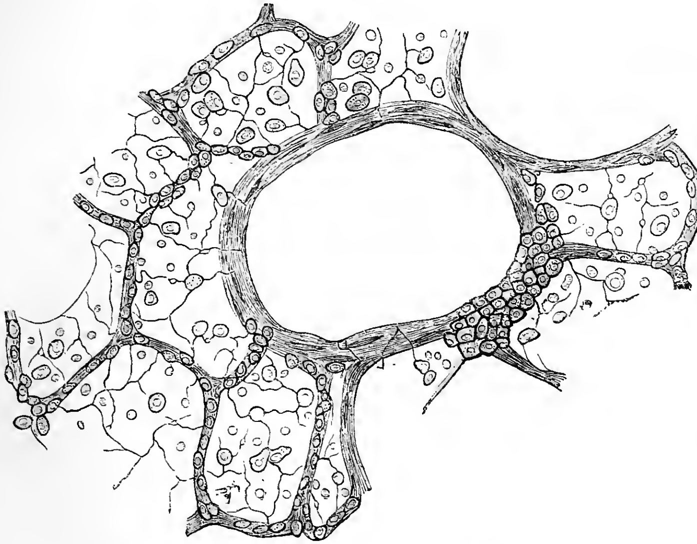


Fig. 447.—Section of part of cat's lung, stained with nitrate of silver (Klein and Noble Smith). Highly Magnified.

The small granular and the large flattened cells of the alveoli are shown. In the middle is a section of a lobular bronchial tube, with a patch of the granular pavement epithelium-cells on one side.

cells, between the others, and always in the interstices of the capillary network.

In the fœtus the alveoli are entirely lined with small granular pavement cells, but with the distension which follows upon the first respiratory efforts most of the cells become transformed into the large thin epithelial elements above described.

The walls of the alveoli, which mainly consist of an indistinctly fibrillated connective tissue with corpuscles scattered here and there, are supported and strengthened by scattered and coiled elastic fibres, especially numerous near their orifices, in addition to which, according to Moleschott and others, there is likewise an intermixture of muscular fibre-cells. A number of granular rounded amœboid cells are usually to be found free in the air-cells and smaller bronchial tubes: not unfrequently they contain carbonaceous particles. By the migration of these cells into the pulmonary tissue, the carbon particles may be conveyed into the substance of the lung and thence into the lymphatics and

bronchial glands, but fluids and fine particles can also, it is believed, penetrate directly to the lymphatics, both of the interalveolar tissue and of the bronchial tubes, by aid of the pseudostomata which connect the cell-spaces of the connective tissue with the inner surface of the mucous membrane (see p. 521).

The air-cells in the natural state, are always filled with air. They are readily seen on the surface and in a section of a lung, which has been inflated with air and dried; also upon portions of fœtal or adult lung injected with mercury or

Fig. 448.

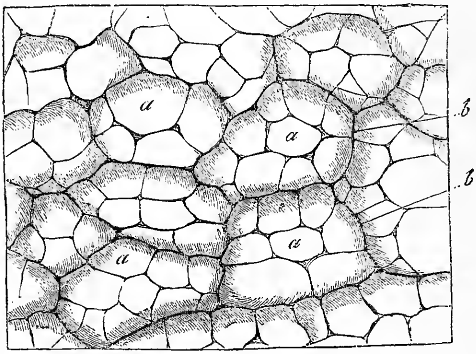


Fig. 448.—Portion of the outer surface of the cow's lung (from Kölliker after Harting). Magnified 30 diameters.

a, pulmonary vesicles filled artificially with wax; *b*, the margins of the smallest lobules or infundibula.

wax (fig. 448, *a*, *a*). In the lungs of some animals, as of the lion, cat, and dog, they are very large, and are distinctly visible on the surface of the organ. In the adult human lung their most common diameter is about $\frac{1}{100}$th of an inch (0·25 mm.), but it varies from $\frac{1}{150}$th to $\frac{1}{70}$th of an inch; they are larger on the surface than in the interior, and largest towards the thin edges of the organ: they are also very large at the apex of the lung. Their dimensions go on increasing from birth to old age, and they are larger in men than in women. In the infant the diameter is usually under $\frac{1}{200}$th of an inch.

The whole lung has a lobulated structure best seen in the fœtus, where the lungs, not yet distended with air, present very much the appearance of compound racemose glands. The infundibula may be regarded as corresponding to the smallest or ultimate lobules of such a gland. They produce the appearance of polygonal areas enclosing groups of six or eight air-cells which are seen at the surface of the lung (fig. 448). The infundibula are grouped into larger or secondary lobules, and these again into yet larger divisions. The various lobules are united and separated by connective tissue in variable amount, more between the larger and less between the smaller groups. From the mutual compression to which they are subjected the lobules are bounded by flattened sides, and they are compactly fitted to each other and to the larger air-tubes and vessels of the lungs.

BLOOD-VESSELS, LYMPHATICS, AND NERVES OF THE LUNGS.

Pulmonary vessels.—The branches of the pulmonary artery accompany the bronchial tubes, but in their remote ramifications they subdivide more frequently. The main arterial trunk runs down immediately behind the main bronchial trunk, giving off corresponding branches as

it proceeds. They ramify without anastomoses, and at length terminate in small arteries about $\frac{1}{1000}$th of an inch in diameter, which lie between the alveoli, partially encircling their mouths (fig. 449, *b*). From these vessels the capillary network arises, and covers each alveolus, passing in the inter-alveolar septa between the adjacent air-cells. As was pointed

Fig. 449.

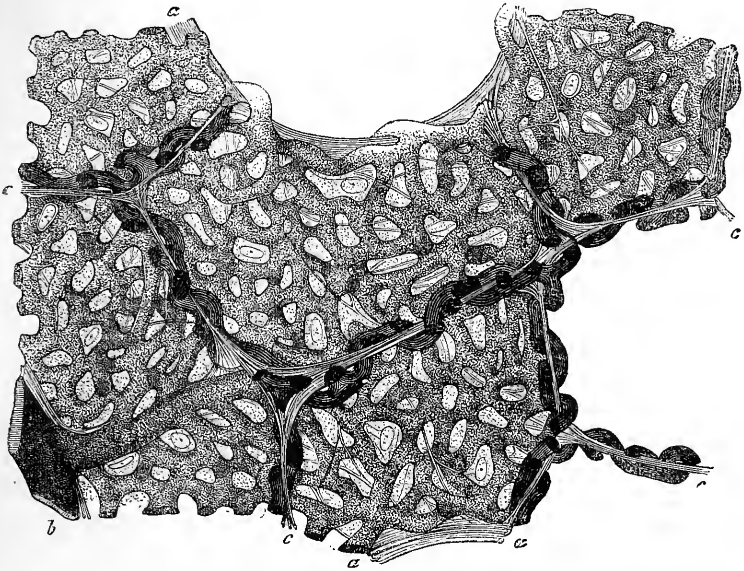


Fig. 449.—Section of injected lung, including several contiguous alveoli (F. E. Schultze). Highly magnified.

a, a, free edges of alveoli; *c, c,* partitions between neighbouring alveoli, seen in section; *b,* small arterial branch giving off capillaries to the alveoli. The looping of the vessels to either side of the partitions is well exhibited. Between the capillaries is seen the homogeneous alveolar wall with nuclei of connective tissue corpuscles, and elastic fibres.

out by Rainey, the capillary network in these partitions is single in the lungs of man and mammalia, although it forms a double layer in the lungs of amphibia and reptiles.

The capillaries are very fine, and the network they form is so close that the meshes are scarcely wider than the vessels themselves. They are very superficial, being covered only by the thin layer of tesselated epithelium above mentioned, and in the partitions between contiguous alveoli the vessels of the network project on either side in an arched or loop-like manner into the cavities of the alveoli (fig. 449). The mucous membrane of the bronchial tubes, especially near the air-cells, is partly supplied with blood from branches of the pulmonary artery.

The radicles of the pulmonary veins arise from the capillary network of the alveoli and from that of the smaller bronchial tubes. The branches of these veins which arise from the infundibula near the surface of the lung, do not accompany the bronchia and arterial branches, but are found to run alone for a certain distance through the substance of

the organ. They finally either join some deeper vein which accompanies a bronchial tube, or they remain superficial, forming a wide-meshed plexus near the surface of the lung, finally tending towards the hilus to join the larger veins near the root of the lung. The veins from the more deeply lying infundibula form frequent communications, and finally coalesce into large branches, which accompany the bronchial tubes and arteries, coursing as a rule in front of the bronchial tubes, and thus proceed to the root of the lung. In their course together through the lung, the artery is usually found above and behind a bronchial tube, and the vein below and in front.

The pulmonary vessels differ from the systemic in regard to their contents, inasmuch as the arteries convey dark blood, whilst the veins carry red blood. The pulmonary veins, unlike the other veins of the body, are not more capacious than their corresponding arteries; indeed, according to Winslow, Santorini, Haller, and others, they are somewhat less so. These veins have no valves. Lastly, it may be remarked that, whilst the arteries of different secondary lobules are usually independent, the veins freely anastomose.

Bronchial vessels.—The bronchial arteries and veins, which are much smaller than the pulmonary vessels, carry blood for the nutrition of the lung. The bronchial arteries, from one to three in number for each lung, arise from the aorta, or from an intercostal artery, and follow the divisions of the air-tubes through the lung. They are ultimately distributed in three ways: (1) many of their branches ramify in the bronchial lymphatic glands, the coats of the large blood-vessels, and in the walls of the bronchial tubes, supplying an outer capillary plexus with transverse meshes to the muscular coat, and an inner plexus with close longitudinal meshes to the mucous membrane, which at the extremities of the bronchial tubes is continuous with that supplied by the pulmonary artery; (2) others form plexuses in the interlobular areolar tissue; (3) branches spread out upon the surface of the lung beneath the pleura, forming plexuses and a capillary network.

A few small branches of the intercostal arteries also pass to the pulmonary pleura and surface of the lung through the ligamentum latum pulmonis (Turner).

The bronchial veins have not quite so extensive a distribution in the lung as the bronchial arteries, since part of the blood carried by the bronchial arteries is returned by the pulmonary veins. The superficial and deep bronchial veins unite at the root of the lung, opening on the right side into the large azygos, and on the left usually into the left upper azygos vein.

According to Zuckerkandl it is not only at the extremities of the bronchial tubes that the blood brought by the bronchial arteries is returned by the pulmonary veins, but in other parts small bronchial veins open into pulmonary branches; and even veins which receive branches from the larger bronchia, from the bronchial glands and from the posterior surface of the pericardium, empty their contents partly into the great trunks of the pulmonary veins.

Lymphatics.—Part of the lymphatics of the lung take origin from lymphatic capillaries in the interalveolar septa, and those near the surface of the lung come into connection with the subpleural lymphatic plexus, previously mentioned (p. 503). They join to form vessels which

accompany the branches of the pulmonary artery and vein, running on the walls of those vessels in twos or threes, connected by numerous cross branches, and in some cases almost completely surrounding the blood-vessel.

Other lymphatics, which might be distinguished as bronchial, originate in plexuses in the mucous membrane of the bronchial tubes. Hence they pass through the muscular coat to form another plexus in the fibrous layer, where they are most numerous on the side opposite the accompanying branch of the pulmonary artery. Here they are not unfrequently found to enclose nodules of lymphoid tissue (see p. 214). The branched connective tissue corpuscles and cell-spaces with which the lymphatics are in connection at their origin, send processes upwards to the inner surface of the air tubes and alveoli, between the epithelial cells (like the pseudostomata of the serous membranes, p. 216). Lymphoid tissue is found, according to Arnold, in various parts, viz., under the pulmonary pleura; in the perivascular and peribronchial tissue; in the bronchial wall, and around the alveolar passages.

At the root of the lung the superficial and deep lymphatics unite into a few anastomosing trunks before entering the bronchial lymphatic glands.

Nerves.—The nerves of the lung come from the anterior and posterior pulmonary plexuses which are formed chiefly by branches from the pneumogastric nerves, joined by others from the sympathetic system. The fine nervous cords enter at the root of the lung, and follow the air-tubes. According to Remak, whose account has been confirmed and added to by the more recent observations of Stirling and others, they include both white fibres, derived in all probability from the vagus, and grey filaments proceeding from the sympathetic, and have ganglion-cells, both singly and in groups, upon them in their course. In the lower vertebrates (frog, newt) the nerves are chiefly distributed to a layer of plain muscular tissue, which is everywhere found taking part in the composition of the relatively simple pulmonary wall (Stirling), but in mammals the final distribution of the nerves requires further examination.

Recent Literature of the lungs and trachea.—(For older literature see the article "Lung" by *F. E. Schultze*, in Stricker's Handbook, 1871); *Rindfleisch*, Muskul. d. kl. Bronchien, Med. Centralbl., 1872; Verästel. d. Art. pulm., Berl. klin. Wochenschr., 1872; *Tarchette*, on the glands of the trachea, in Riv. d. med. &c. di Soresina, 1874; *Aufrecht*, Epith. d. Lungenalv., Med. Centralbl., 1875; *Küttner*, Lungenepith., Virch. Arch., 1876; Kreislauf d. Lunge, Virch. Arch. LXXIII., 1878; *Cohnheim u. Litten*, Emb. d. Lungenarterien, Virch. Arch., LXV., 1876; *Cadiat*, Rapp. entre le dével. du poumon et sa structure, Arch. de physiol., 1877; *Stirling*, Nervous apparatus of the lung, Brit. Med. Journal, 1876; Proc. Roy. Soc., 1880, and Journ. of Anat., 1881; Hyperplasia of muscular tissue of lung, Journal of Physiol., 1878; *Aeby*, Bronchial-baum, Med. Centralbl., 1878, and Leipzig, 1880; *Sée*, Calibre de la trach. et des bronches, Rev. d. sc. med. XII., 1878; *Frankenhäuser*, Tracheo-bronchial-schleimhaut, Diss., Dorpat., 1879; *Veraguth*, Lungenepith., Virch. Arch., LXXXII., 1880; *Kölliker*, Bau d. menschl. Lunge, Wurzb. Verhandl., 1881; *Kandarazi*, on the nerves of the respir. tubes, in Arch. f. Anat., 1881; *Zuckerkandl*, in Wiener Sitzungsb., 1881.

On the lymphatics of the lungs. — *Sikorski*, in Med. Centralbl., 1870; *Klein*, Anatomy of Lymphatic System, Part II., 1875; *Ins*, in Arch. f. exp. Pathol., V. 1876, and in Virch. Arch., LXXIII., 1878; *Nothnagel* in Virch. Arch., LXXI., 1877; *Grancher* in Gaz. méd., 1877; *Ruppert* in Virch. Arch., LXXII., 1878; *Schottelius* in Virch. Arch. LXXIII., 1878; *v. Wittich*, in Mitth. a. d. Konigsb. physiol. Laborat., 1878; *Schestopal* in Virch. Arch., LXXV., 1879; *J. Arnold*, in Virch. Arch., LXXX., 1880.

THE LARYNX, OR ORGAN OF VOICE.

The **larynx** is placed at the upper and fore part of the neck, where it forms a considerable prominence in the middle line. It lies between the large vessels of the neck, and below the tongue and hyoid bone. It is covered in front by the cervical fascia along the middle line, and on each side by the sterno-hyoid, sterno-thyroid, and thyro-hyoid muscles, by the upper end of the thyroid body, and by a small part of the inferior constrictor of the pharynx. Behind it, is the pharyngeal mucous membrane, and above, it opens into the cavity of the pharynx.

The larynx consists of a framework of cartilages, articulated together, and connected by elastic membranes or ligaments, two of which projecting into the interior of the cavity are named the *true vocal cords*, being more immediately concerned in the production of the voice. It possesses special muscles, which move the cartilages one upon another, and modify its form and the tension of its ligaments, and it is lined by a mucous membrane, continuous above with the mucous membrane of the pharynx and below with that of the trachea.

CARTILAGES OF THE LARYNX.

The cartilages of the larynx (fig. 450, 451) consist of three single and symmetrical prices, named respectively the *thyroid cartilage* (4), the *cricoid cartilage* (fig. 450, 8, fig. 451, 2), and the *cartilage of the epiglottis* (fig. 451, 7), and of three pairs, namely, the two *arytenoid cartilages* (fig. 451, 3), the *cornicula laryngis*, and the *cuneiform cartilages*. In all there are nine distinct pieces, but the cornicula and cuneiform cartilages are very small. Only the thyroid and cricoid cartilages are visible on the front and sides of the larynx; the back of the cricoid cartilage surmounted by the arytenoid cartilages and these again by the cornicula are seen at the back, whilst the epiglottis is situated in front of, and the cuneiform cartilages on each side of the upper opening.

The **thyroid** cartilage, the largest, consists of two flat lateral plates which are continuous in front, forming a narrow angle with one another like the letter V, most prominent at the upper part. This angular projection is subcutaneous, and is much more marked in the male than in the female, being named in the former the *pomum Adami*. The two symmetrical halves, named the *alæ*, are somewhat quadrilateral in form. Of each half the anterior border is the shortest, the pomum Adami being surmounted by a deep notch (see fig. 450). The free posterior border is thickened and vertical, and is prolonged upwards and downwards into two processes or *cornua*; it gives attachment to the stylo-pharyngeus and palato-pharyngeus muscles. The upper and lower border have each a well-marked sinuosity close to the cornu: otherwise the upper is convex, and the lower nearly straight. The flattened external surface of each ala is marked by an indistinct oblique line or ridge (fig. 450), which, commencing at a tubercle, situated at the back part of the upper border, passes downwards and forwards to a tubercle below, so as to mark off the anterior three-fourths of the surface from the remainder. This line gives attachment below to the sterno-thyroid, and above to the thyro-hyoid muscle, whilst the small smooth surface behind it, gives origin to part of the inferior constrictor of the pharynx, and affords

attachment by means of areolar tissue, to the thyroid body. On their internal surfaces, the alæ are smooth and slightly concave. Of the four cornua, all of which bend inwards, the two *superior* or *great* cornua (fig. 450), pass upwards with sometimes a slight backward curve, and terminate each by a blunt extremity, which is connected, by means of the lateral thyro-hyoid ligament, to the tip of the corresponding great cornu

Fig. 450.

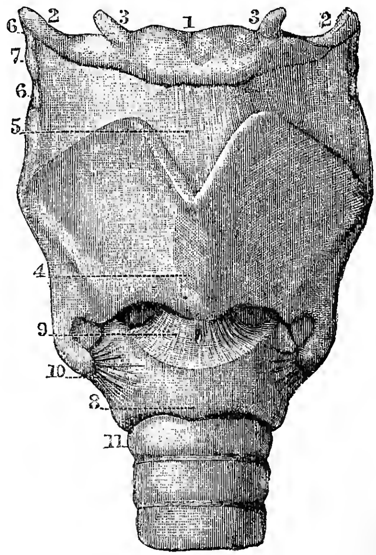


Fig. 450.—Front view of the laryngeal cartilages and ligaments (Sappey).

1, hyoid bone; 2, its large cornua; 3, its small cornua; 4, thyroid cartilage; 5, thyro-hyoid membrane; 6, lateral thyro-hyoid ligament, containing the *cartilago triticea*, 7; 8, cricoid cartilage; 9, crico-thyroid membrane; 10, lateral crico-thyroid ligaments.

of the hyoid bone (fig. 450, 2). The *inferior* or *smaller* cornua, which are somewhat thicker but shorter, are directed slightly forwards, and, on the inner aspect of the tip, present a smooth surface, for articulation with a prominence on the side of the cricoid cartilage.

The **cricoid** cartilage (fig. 450, 8), which is shaped like a signet ring, is thicker and stronger than the thyroid. It is deep behind (fig. 451, 2), where it is expanded into a squarish plate or lamina, measuring in the male about an inch from above downwards; but in front it forms a narrow ring or arch, with a vertical measurement of only one-fourth or one-fifth of an inch. Corresponding with this, the *superior border*, which is markedly elevated behind, descends with a deep concavity in front below the thyroid cartilage; while the *inferior border*, is horizontal, and connected by membrane to the first ring of the trachea. The posterior elevated part of the upper border is slightly depressed in the middle line; and on the sides of this depression are the elongated oval facets for articulation with the arytenoid cartilages. These facets are slightly convex and they look outwards as well as upwards. The *external surface* of the cartilage is convex and smooth in front and at the sides, where it affords attachment to the crico-thyroid muscles, and behind these to the inferior constrictors of the pharynx: in the middle line posteriorly is a slight vertical ridge to which some of the longitudinal fibres of the œsophagus are attached. On each side of this ridge is a broad depression occupied by the posterior crico-arytenoid muscle, outside which is a small concave rounded and slightly raised surface for articulation with the inferior cornu of the thyroid cartilage (fig. 458). The *internal surface* is covered throughout by the mucous membrane of the larynx. At its lower border the cricoid is cir-

cular, but higher up the cartilage is somewhat compressed laterally, so that the passage through it is here elliptical.

The **arytenoid** cartilages (fig. 451, 3) are two in number, and symmetrical in form and position. They may be compared in shape to irregular three-sided pyramids, and they rest by their bases on the posterior and highest part of the cricoid cartilage, while their somewhat curved apices approach one another. Each is about half an inch high, and one quarter of an inch wide. Of the three faces the *posterior* is broad, triangular, and concave from above downwards, lodging part of the arytenoid

Fig. 451.

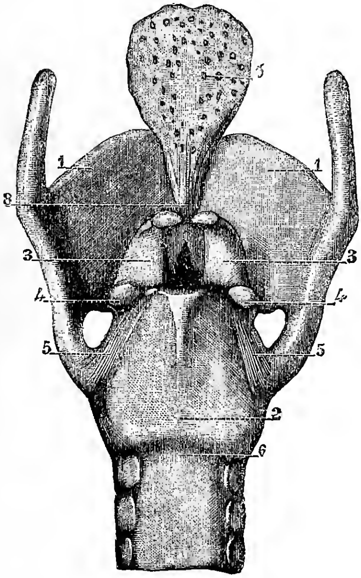


Fig. 451.—Back view of the laryngeal cartilages and ligaments (Sappey).

1, thyroid cartilage ; 2, cricoid cartilage ; 3, arytenoid cartilages ; 4, their muscular processes ; 5, a ligament better marked than usual, connecting the lower cornu of the thyroid with the back of the cricoid cartilage ; 6, upper ring of the trachea ; 7, epiglottis ; 8, ligament connecting it to the angle of the thyroid cartilage. The cornicula are seen surmounting the arytenoid cartilages.

muscle. The *anterior*, or *external*, convex in its general outline, and somewhat rough, gives attachment to the thyro-arytenoid muscle, and, by a small tubercle, to the corresponding superior or false vocal cord. The *internal* surface, which is the narrowest of the three, and slightly convex, is nearly parallel with that of the opposite cartilage, and is covered by the laryngeal mucous membrane. The anterior and posterior borders, which limit the internal face, are nearly vertical, whilst the external border, which separates the anterior from the posterior surface, is oblique.

The *base* of each arytenoid cartilage is slightly hollowed, having towards its outer part a smooth surface for articulation with the cricoid cartilage. Two of its angles are remarkably prominent, viz., one *external*, short, and rounded, which projects backwards and outwards, and into which the posterior and the lateral crico-arytenoid muscles are inserted (*muscular process*) ; the other *anterior*, which is more pointed, and forms a horizontal projection forwards, to which the corresponding true vocal cord is attached (*vocal process*).

The *apex* curves backwards and a little inwards, and terminates in a blunt point, which is surmounted by the corniculum laryngis.

A small cartilaginous nodule (sesamoid cartilage) is sometimes found at the side of the arytenoid near the tip, embedded in the perichondrium.

The **cornicula laryngis,** or **cartilages of Santorini,** are two small yellowish cartilaginous nodules of a somewhat conical shape, which are

articulated with the summits of the arytenoid cartilages (fig. 451), and serve as it were to prolong them backwards and inwards. They sometimes form part of the arytenoid cartilages.

The **cuneiform cartilages,** or **cartilages of Wrisberg,** are two very small, soft, yellowish, cartilaginous bodies, placed, one on each side, in the fold of the mucous membrane which extends from the summit of the arytenoid cartilage to the epiglottis. They have a conical form, with the base directed upwards. They occasion small elevations of the mucous membrane, a little in advance of the cornicula, with which, however, they are not directly connected.

These cartilages are very frequently absent, especially in the white races of mankind, but according to Gibb are always present in the negro.

The **epiglottis** (fig. 451, 7) is a median lamella of yellow cartilage, shaped somewhat like an obovate leaf, and covered by mucous membrane. It is placed in front of the superior opening of the larynx, projecting, in the ordinary condition, upwards immediately behind the base of the tongue ; but during the act of swallowing it is carried downwards and backwards over the entrance into the larynx, which it covers and protects.

The cartilage of the epiglottis is broad and rounded at its upper free margin, but inferiorly it becomes pointed, and is prolonged by means of a long, narrow, elastic band (the *thyro-epiglottic ligament*) to the deep angular depression between the alæ of the thyroid cartilage, to which it is attached behind and below the median notch. Its *lateral* borders, which are convex and turned backwards, are only partly free, the lower parts being enveloped in the aryteno-epiglottic folds of mucous membrane. The *anterior* or *lingual* surface is free only in its upper part, where it is covered by mucous membrane. Lower down, the membrane is reflected from it forwards to the base of the tongue, forming three folds or frænula, the middle and lateral glosso-epiglottic folds. This surface is also connected below with the posterior surface of the hyoid bone by a median elastic structure named the *hyo-epiglottic ligament.* The *posterior* or *laryngeal* surface, which is free in the whole of its extent, is concavo-convex from above downwards, but concave from side to side : the convexity projecting backwards into the larynx is named the tubercle or cushion. The epiglottis is closely covered by mucous membrane, on removing which, the yellow cartilaginous lamella is seen to be pierced by numerous little pits and perforations, in which are lodged small glands which open on the surface of the mucous membrane.

Up to the age of puberty the larynx is similar in the male and female, the chief characteristics at that period being the small size and comparative slightness of the organ, and the smooth rounded form of the thyroid cartilage in front. In the female these conditions are permanent, excepting that a slight increase in size takes place. In the male, on the contrary, at the time of puberty, remarkable changes rapidly occur, and the larynx becomes more prominent and more perceptible at the upper part of the neck. Its cartilages become larger, thicker, and stronger, and the alæ of the thyroid cartilage project forwards in front so as to form at their union with one another, the prominent ridge of the *pomum Adami.* At the same time, the median notch on its upper border is considerably deepened. In consequence of these changes in the thyroid cartilage, the distance between its angle in front and the arytenoid

cartilages behind becomes greater, and the vocal cords are necessarily lengthened. Hence the dimensions of the glottis, which, at the time of puberty, undergo an increase of about one-third only in the female, are nearly doubled in the male, and the adult male larynx becomes altogether one-third larger than that of the female.

Towards the middle of life the cartilages of the larynx first show a tendency to ossification; this commences first in the thyroid cartilage, then appears in the cricoid, and much later in the arytenoid cartilages. In the thyroid cartilage the ossification usually begins at the cornua and posterior borders; it then gradually extends along the whole inferior border, and subsequently spreads upwards through the cartilage. The cricoid cartilage first becomes ossified at its upper border upon each side, near the two posterior articular eminences, and the ossification invades the lateral parts of the cartilage before encroaching either on the anterior or posterior parts. The arytenoid cartilages become ossified from below upwards.

Structure of the cartilages of the larynx.—The epiglottis, the cornicula laryngis and the cuneiform cartilages, are composed of elastic or yellow fibro-cartilage (p. 82), and have little tendency to ossify. The apices of the arytenoid cartilages are also formed of elastic fibro-cartilage, but the greater part of these, as well as the cricoid and thyroid cartilage are composed of hyaline cartilage, resembling generally that of the costal cartilages (p. 81), like which, they are very prone to ossification as life advances.

LIGAMENTS AND JOINTS OF THE LARYNX.

The larynx is connected with the hyoid bone by a broad membrane and at the sides of this by two round lateral ligaments. The **thyro-hyoid membrane** or **middle thyro-hyoid ligament** (fig. 450, 5), is a broad, fibrous, and somewhat elastic membrane, which passes up from the whole length of the superior border of the thyroid cartilage to the hyoid bone, where it is attached to the posterior and upper margin of the obliquely inclined inferior surface. Owing to this arrangement, the top of the larynx, when drawn upwards, is permitted to slip within the circumference of the hyoid bone, between which and the upper part of the thyroid cartilage there is occasionally found a small synovial bursa. The thyro-hyoid membrane is thick where subcutaneous towards the middle line, out at the sides becomes thin and loose, and is covered by the thyro-hyoid muscles. Behind is the epiglottis with the mucous membrane of the base of the tongue, separated, however, by adipose tissue and mucous glands. This ligament is perforated by the superior laryngeal artery and nerve of each side. The **lateral thyro-hyoid ligaments** (fig. 450, 6), placed at the posterior limits of the thyro-hyoid membrane, are two rounded yellowish cords, which pass up from the superior cornua of the thyroid cartilage, to the extremities of the great cornua of the hyoid bone. They are distinctly elastic, and there is frequently enclosed in each a small oblong cartilaginous nodule, which has been named *cartilago triticea:* sometimes this nodule is bony.

The thyroid and cricoid cartilages are connected together by a membranous ligament and synovial articulations. The **crico-thyroid membrane** (fig. 450, 9) is divisible into a mesial and two lateral portions. The mesial portion, broad below and narrow above, is a strong triangular yellowish ligament, consisting chiefly of elastic tissue, and is attached

to the contiguous borders of the two cartilages. Its anterior surface is convex, is partly covered by the crico-thyroid muscles, and is crossed horizontally by a small anastomotic arterial arch, formed by the junction of the crico-thyroid branches of the right and left superior thyroid arteries. The lateral portions are fixed on each side along the inner edge of the upper border of the cricoid close under the mucous membrane; they become much thinner above, where they are continuous with the inferior thyro-arytenoid ligaments.

The **crico-thyroid articulations**, between the inferior cornua of the thyroid cartilage and the sides of the cricoid, are two small but distinct joints, having each a ligamentous capsule and a synovial membrane. The prominent oval articular surfaces of the cricoid cartilage are directed upwards and outwards, while those of the thyroid cartilage, which are slightly concave, look in the opposite direction. The capsular fibres form a stout band behind the joint. The movement allowed is of a rotatory description, the axis of rotation passing transversely through the two joints. In addition, a slight gliding movement in different directions may occur.

The **superior thyro-arytenoid ligaments** consist of a few slight fibrous fasciculi, contained within the folds of mucous membrane forming the false vocal cords hereafter to be described, and are fixed in front to the angle between the alæ of the thyroid cartilage, somewhat above its middle, and close to the attachment of the epiglottis: behind, they are connected to the tubercles on the rough anterior surface of the arytenoid cartilages. They are continuous above with scattered fibrous bundles contained in the aryteno-epiglottidean folds.

The **inferior thyro-arytenoid ligaments** are formed of fine closely arranged elastic fibres which are attached in front to the middle of the angle between the alæ of the thyroid cartilage, and behind to the anterior projection of the base of the arytenoid cartilages. The inner edge of each ligament is free and sharply defined between those attachments, and, covered by their mucous membrane, forms the *true vocal cord* of its own side. In other directions these ligaments are less sharply defined, for in their outer part they spread out both above and below as they pass backwards. Above, the fibres of the ligament lie near the upper surface of the projecting fold of mucous membrane which bounds the rima glottidis, and become gradually merged into the elastic tissue of that membrane. Below, the inferior thyro-arytenoid ligament passes into continuity with the lateral crico-thyroid ligament, so that it may be described as an upward extension of this ligament, and the vocal cord may be stated to be formed by the superior free edge of the crico-thyroid membrane.

The **crico-arytenoid articulations** are surrounded by a series of thin capsular fibres, which, together with a loose synovial membrane, serve to connect the convex elliptical articular surfaces on the upper border of the cricoid cartilage with the concave articular depressions on the bases of the arytenoid cartilages. The articular surface on the arytenoid cartilage is longer from before back than from side to side; so that its long axis crosses that of the corresponding surface on the cricoid, and a part of the latter surface is in every position of the arytenoid left uncovered (Henle). The movements allowed are of two kinds, viz.;—1. a lateral gliding movement from within out or vicê versâ, the arytenoid cartilage being bodily moved away from or towards its fellow; 2. a

rotating movement on a nearly vertical axis, the vocal processes being inclined inwards or outwards (as well as somewhat downwards or upwards). A combined rotating and gliding movement may also occur. The ordinary position of the arytenoid, when the larynx is at rest, is on the outer part of the articular surface on the cricoid. There is a strong **crico-arytenoid ligament,** arising from the cricoid, and inserted into the inner and back part of the base of the arytenoid cartilage.

The summits of the arytenoid cartilages and the cornicula laryngis are sometimes united by a synovial joint, but most frequently by connective tissue forming a sort of synchondrosis.

INTERIOR OF THE LARYNX.

The cavity of the larynx is divided into an upper and a lower compartment by the comparatively narrow aperture of the glottis, or *rima glottidis,* the margins of which, in their two anterior thirds are formed by the lower or *true vocal cords;* and the whole laryngeal cavity, viewed in transverse vertical section (fig. 452) thus presents the appearance of an hour-glass. The upper compartment communicates with the pharynx by the *superior aperture* of the larynx, and contains immediately above the rima glottidis the *ventricles* (*s*), with their pouches or *saccules,* and the upper or *false vocal cords.* The lower compartment passes inferiorly into the tube of the windpipe without any marked constriction or limitation between them. The whole of the interior of the larynx is lined by mucous membrane.

Fig. 452.

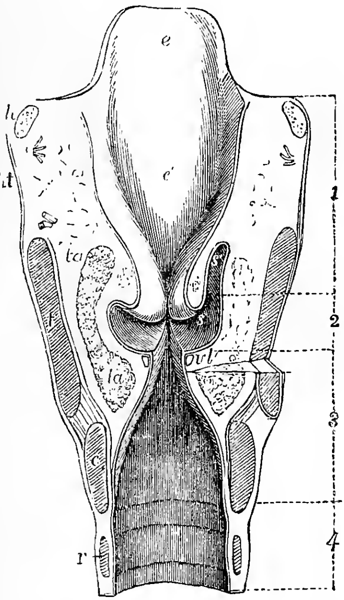


Fig. 452.—Anterior half of a transverse vertical section through the larynx near its middle (Allen Thomson).

1, upper division of the laryngeal cavity; 2, central portion; 3, lower division, continued into 4, trachea; *e*, the free part of the epiglottis; *e'*, its cushion; *h*, great cornua of the hyoid bone; *ht*, thyro-hyoid membrane; *t*, thyroid cartilage; *c*, cricoid cartilage; *r*, first ring of the trachea; *ta*, thyro-arytenoid muscle; *vl*, inferior thyro-arytenoid ligament in the membrane of the true vocal cord at the rima glottidis; *s*, the ventricle; above this, the superior or false cords; *s'*, the sacculus or pouch opened on the right side by carrying the section further forward.

The **superior aperture** of the larynx is triangular, wide in front and narrow behind, the lateral margins sloping obliquely downwards and backwards. It is bounded in front by the epiglottis (fig. 453, A, *e*, and fig. 454, *a*), behind by the summits of the arytenoid cartilages (fig. 453, B, *a*) and cornicula (*s*) with the angular border of mucous membrane crossing the median space between them, and on the sides by two folds of mucous membrane, the *aryteno-epiglottic folds,* which, enclosing a

few ligamentous and muscular fibres and the cuneiform cartilages, pass forwards from the tips of the arytenoid cartilages and cornicula to the lateral margins of the epiglottis (fig. 454, 8, 9, 10).

In studying the form of the laryngeal cavity, and its apertures, it is well to become acquainted with the appearances which they present on examination during life by means of the laryngoscope, and with the relations of these to the

Fig. 453.

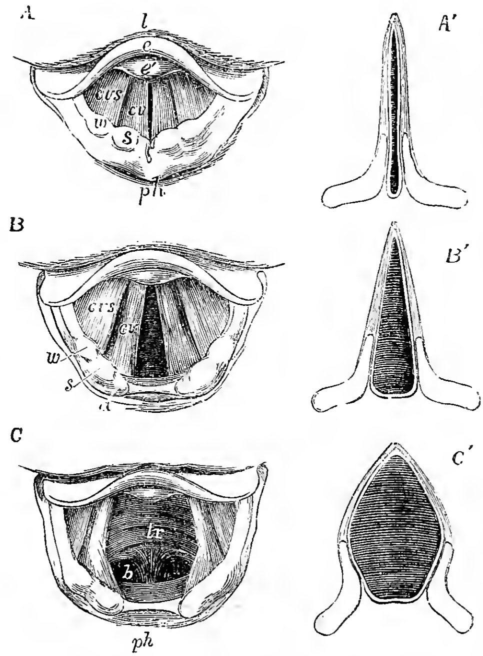


Fig. 453.—Three laryngoscopic views of the superior aperture of the larynx and surrounding parts in different states of the glottis during life (from Czermak).

A, the glottis during the emission of a high note in singing. B, in easy or quiet inhalation of air. C, in the state of widest possible dilatation as in inhaling a very deep breath. The diagrams A', and C' (A.T.), have been added to Czermak's figures to show in horizontal sections of the glottis the position of the vocal ligaments and arytenoid cartilages in the three several states represented in the other figures. In all the figures, so far as marked, the letters indicate the parts as follows, viz.: *l*, the base of the tongue; *e*, the upper free part of the epiglottis; *e'*, the tubercle or cushion of the epiglottis; *p h*, part of the anterior wall of the pharynx behind the larynx; in the margin of the aryteno-epiglottidean fold *w*, the swelling of the membrane caused by the cuneiform cartilage; *s*, that of the corniculum; *a*, the tip of the arytenoid cartilages; *c v*, the true vocal cords or lips of the rima glottidis; *c v s*, the superior or false vocal cords; between them the ventricle of the larynx; in C, *t r* is placed on the anterior wall of the receding trachea, and *b* indicates the commencement of the two bronchi beyond the bifurcation, which may be brought into view in this state of extreme dilatation.

anatomical structure. On thus examining the superior aperture, there are seen on each side two rounded elevations (fig. 453, *s*, *w*), corresponding respectively to the cornicula and the cuneiform cartilages; while in the middle line in front there is a tumescence of the mucous membrane on the lower part of the epiglottis, enabling that structure to close the aperture more accurately when it is depressed, and named the *tubercle* or *cushion of the epiglottis* (*e'*). The mucous membrane between the arytenoid cartilages is stretched when they are separated (B, C), and folded double when they are approximated (A).

On looking down through the superior opening of the larynx, the *glottis* or *rima glottidis* (fig. 454, *c*) is seen at some distance below, in the form of a long narrow fissure running from before backwards. It is situated on a level with the lower part of the arytenoid cartilages, and is bounded by the *true vocal*

cords. Above the glottis, another pair of projecting folds is seen, the *superior* or *false vocal cords*, which are much less projecting than the inferior. Between the superior and inferior vocal cords, the *sinus* or *ventricle* is seen as an elongated depression (fig. 452, *s*, and fig. 454, *b'*).

The **superior vocal cords**, also called the *false* vocal cords, because they are not immediately concerned in the production of the voice, are prominent rounded folds of mucous membrane enclosing very numerous glands which form somewhat arched projections, immediately above the corresponding ventricle (fig. 454, *b*). The latter is seen on looking down into the laryngeal cavity, the superior vocal cords (*cvs*, fig. 453) being further apart than the inferior.

Fig. 454.

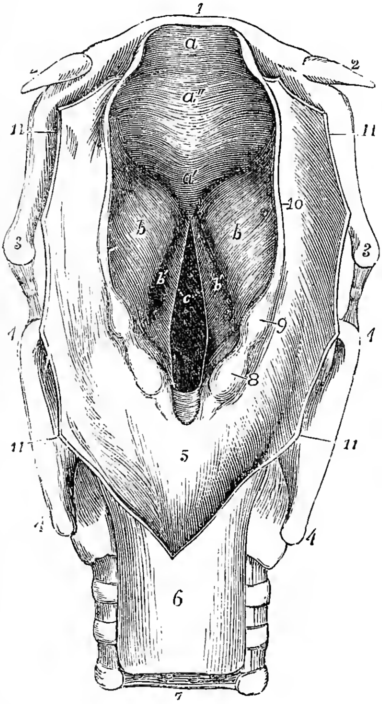


Fig. 454.—Perspective view of the pharyngeal opening into the larynx from above and behind (Allen Thomson).

The superior aperture has been much dilated; the glottis is in a moderately dilated condition; the wall of the pharynx is opened from behind and turned to the sides. 1, body of the hyoid bone; 2, small cornua; 3, great cornua; 4, cornua of the thyroid cartilage; 5, membrane of the pharynx covering the posterior surface of the cricoid cartilage; 6, gullet; 7, trachea; 8, projection caused by the cartilage of Santorini; 9, the same belonging to the cartilage of Wrisberg; 10, aryteno-epiglottidean fold; 11, cut margin of the wall of the pharynx; *a*, free part of the epiglottis; *a'*, its lower pointed part; *a''*, the cushion; *b*, eminence on each side over the sacculus or pouch of the larynx; *b'*, the ventricles; *c*, the glottis intermembranous part: the lines on each side point to the vocal cords; *d*, intercartilaginous part of the glottis.

The **inferior or true vocal cords**, the structures by the vibration of which the sounds of the voice are produced, bound the two anterior thirds of the aperture of the glottis, corresponding with the thyro-arytenoid ligaments (fig. 454, *c*). The mucous membrane covering them is so thin and closely adherent as to show the yellowish colour of the ligaments through it. Their free edges, which are sharp and straight, and directed upwards, form the lower boundaries of the ventricles, and are the parts thrown into vibration during the production of the voice. Their inner surfaces are flattened, and look towards each other.

The **rima glottidis,** an elongated aperture, situated, anteriorly, between the inferior or true vocal cords, and, posteriorly, between the bases of the arytenoid cartilages, forms a long narrow slit, slightly wider in the centre when nearly closed, as in the production of the voice; when

moderately open, as in easy respiration, its shape is that of a long triangle, the pointed extremity being directed forwards, and the base being behind, between the arytenoid cartilages (fig. 453, B′); in its fully dilated condition it is lozenge-shaped (the posterior sides being formed by the inner sides of the bases of the arytenoid cartilages), while the posterior angle is truncated (C′). The rima glottidis is the narrowest part of the interior of the larynx; in the adult male it measures about 23 mm., or nearly an inch, in an antero-posterior direction, and 6 or 8 mm. across at its widest part, which may be dilated to nearly 12 mm. In the female, and in males before the age of puberty, its dimensions are less, its antero-posterior diameter being about 17 mm., and its transverse diameter about 4 mm. The vocal cords are about 15 mm. long in the adult male, and 11 mm. in the female.

The **ventricles** or **sinuses** of the larynx (fig. 452, *s*, and fig. 454, *b′*) are narrower at their orifice than in their interior. The outer surface of each is covered by the upper fibres of the corresponding thyro-arytenoid muscle.

The small recesses named the *laryngeal pouches* (fig. 452, *s′*), lead from the anterior part of the ventricles upwards, for the space of half an inch, between the superior vocal cords inside and the thyroid cartilage outside, reaching as high as the upper border of that cartilage at the side of the epiglottis. The pouch, which is of variable size, is conical in shape, and curved slightly backwards. Its opening into the ventricle is narrow, and is generally marked by two folds of the lining mucous membrane. Numerous small mucous glands, sixty or seventy in number, open into its interior, and it is surrounded by a quantity of fat. Externally to the fat, this little pouch receives a fibrous investment, which is continuous below with the superior vocal cord. Over its laryngeal side and upper end is a thin layer of muscular fibres (compressor sacculi laryngis, arytæno-epiglottideus inferior, Hilton) connected above with those found in the aryteno-epiglottidean folds. The upper fibres of the thyro-arytenoid muscles pass over the outer side of the pouch, a few being attached to its lower part. The laryngeal pouch is supplied abundantly with nerves, derived from the superior laryngeal.

MUSCLES OF THE LARYNX.

Besides certain extrinsic muscles elsewhere described—viz., the sterno-hyoid, omo-hyoid, sterno-thyroid, and thyro-hyoid muscles, together with the muscles of the suprahyoid region, and the middle and inferior constrictors of the pharynx, all of which act more or less upon the entire larynx—there are other muscles which move the different cartilages upon one another, and modify the size of the apertures and the state of tension of the vocal cords. These intrinsic muscles are the *crico-thyroid*, the *posterior crico-arytenoid*, the *lateral crico-arytenoid*, the *thyro-arytenoid*, the *arytenoid*, and the *aryteno-epiglottidean*, together with certain other slender muscular fasciculi. All these muscles, except the arytenoid which crosses the middle line, are in pairs.

The **crico-thyroid muscle** (fig. 455, 10), is a short thick triangular muscle, seen on the front of the larynx. Its attachment below, to the cricoid cartilage, extends from the median line a considerable way backwards, and its fibres passing upwards and outwards, diverging slightly, are fixed above to the inferior border of the thyroid cartilage, and to the

anterior border of its lower cornu. The latter portion of the muscle, the fibres of which are nearly horizontal, is usually distinct from the rest. Some of the superficial fibres are almost always continuous with the inferior constrictor of the pharynx. The muscles of the two sides are

Fig. 455.

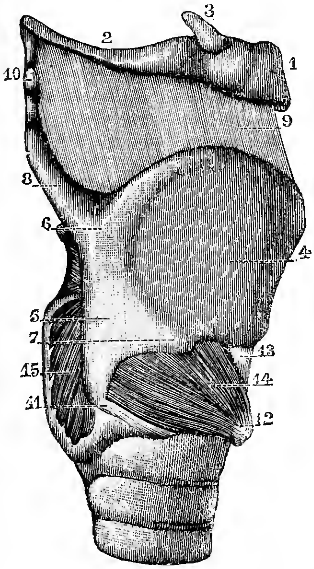


Fig. 456.

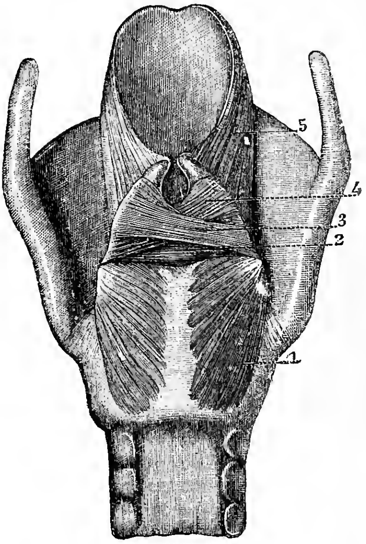


Fig. 455.—Side view of the larynx (Sappey).

1, hyoid bone; 2, 3, its cornua; 4, right ala of thyroid cartilage; 5, posterior part of the same separated by oblique line from anterior part; 6, 7, superior and inferior tubercles at ends of oblique line; 8, upper cornu of thyroid; 9, thyro-hyoid ligament; 10, *cartilago triticea;* 11, lower cornu of thyroid, articulating with the cricoid; 12, anterior part of cricoid; 13, crico-thyroid membrane; 14, crico-thyroid muscle; 15, posterior crico-arytenoid muscle partly hidden by thyroid cartilage.

Fig. 456.—Posterior muscles of the larynx (Sappey).

1, posterior crico-arytenoid; 2, arytenoid muscle; 3, 4, oblique fibres passing around the edge of the arytenoid cartilage to join the thyro-arytenoid, and to form the aryteno-epiglottidean, 5.

somewhat separate from one another in the middle line in front, leaving an interval which is triangular with the base upwards. The crico-thyroid membrane is here exposed.

Action. The anterior part of the muscle contracting will approximate the cricoid and thyroid cartilages in front. In this action the thyroid is fixed by the extrinsic muscles, and the anterior part of the cricoid rotating on the axis which unites the articulations between the cricoid and the lower cornua of the thyroid is drawn upwards, and the part behind the crico-thyroid joints is depressed, and with it the arytenoid cartilages, so that the vocal cords are thus put on the stretch. This stretching of the vocal cords is still further assisted by the action of the oblique fibres, which acting from the cornu of the fixed thyroid, draw the cricoid cartilage backwards. The muscle is generally described as acting from the cricoid, but as Jelenffy has shown, it is the thyroid that is fixed in

vocalization, the cricoid being moveable, and indeed receiving no extrinsic muscles capable of fixing it effectually. It is found also that with electric excitation of this muscle the anterior part of the cricoid is raised towards the thyroid. Paralysis of these muscles is accompanied by inability to produce high tones of the voice.

Fig. 457.

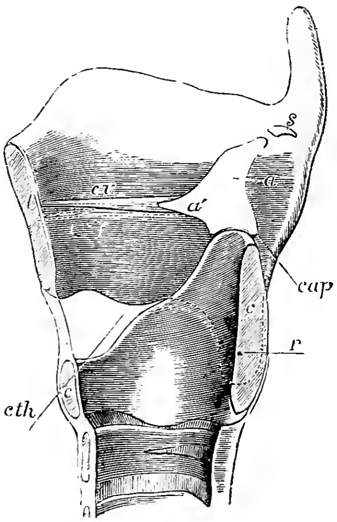


Fig. 457.—Outline of the right half of the cartilages of the larynx as seen from the inside, with the thyro-arytenoid ligament, to illustrate the action of the crico-thyroid muscle (Allen Thomson).

t, thyroid cartilage; *c*, cricoid cartilage; *a*, right arytenoid cartilage; *a'*, its vocal process; *s*, corniculum; *c v*, the thyro-arytenoid ligament; the position of the lower cornu of the thyroid cartilage on the outside of the cricoid is indicated by a dotted outline, and *r* indicates the point or axis of rotation of the cricoid cartilage on the cornu of the thyroid; *c t h*, a line in the principal direction of action of the crico-thyroid muscle; *c a p*, the same of the posterior crico-arytenoid muscle.

The **posterior crico-arytenoid muscle** (fig. 456, 1), situated behind, arises from the broad depression on the corresponding half of the posterior surface of the cricoid cartilage, and its fibres, converging upwards and outwards, are inserted into the outer angle of the base of the arytenoid cartilage, behind the attachment of the lateral crico-arytenoid muscle. The upper fibres are short and almost horizontal; the middle are the longest and run obliquely; whilst the lower or external fibres are nearly vertical.

Action. The posterior crico-arytenoid muscles draw the outer angles of the arytenoid cartilages backwards and inwards, and thus rotate the anterior or vocal processes outwards, and widen the rima glottidis. They may also draw the arytenoid cartilages apart. They come into action during deep inspiration. If paralysed the lips of the glottis approach the middle line, and come in contact with each inspiration, so that severe dyspnoea may be produced. Expiratory efforts, however, are not impeded, and vocalization is unaffected.

Variety.—In connection with the posterior crico-arytenoid muscle, may be mentioned an occasional small slip in contact with its lower border, viz., the **kerato-cricoid** muscle of Merkel. It is a short and slender bundle, arising from the cricoid cartilage near its lower border, a little behind the inferior cornu of the thyroid cartilage, and passing obliquely outwards and upwards to be inserted into that process. It usually exists on only one side. Turner found it in seven out of thirty-two bodies. It is not known to be of any physiological significance. (Merkel, Anat. und Phys. des menschl. Stimm-und Spräch-organs, Leipzig, 1857; Turner in Month. Med. Journal, Feb. 1860.)

The **lateral crico-arytenoid muscle** (fig. 458, *f*), smaller than the posterior, is in a great measure hidden by the ala of the thyroid cartilage. It lies along the sloping upper border of the cricoid cartilage, from which it arises, its origin extending as far back as the articular surface for the

arytenoid. Its fibres pass backwards and upwards, the anterior or upper ones being necessarily the longest, and are attached to the muscular process of the arytenoid cartilage and to the adjacent part of its anterior surface.

This muscle is covered internally by the lateral part of the crico-thyroid membrane, and externally at its anterior part by the upper part of the crico-thyroid muscle. The upper part is in close contact and indeed is sometimes blended with the thyro-arytenoid.

Action. These muscles, drawing the muscular processes of the arytenoid forwards and downwards, rotate the vocal processes inwards, and approximate the vocal cords. They thus act antagonistically to the posterior crico-arytenoid.

If both posterior and lateral crico-arytenoids be thrown into action simultaneously, the arytenoids will not undergo rotation, but will be drawn downwards and outwards, and the glottis will thus be widened.

The **thyro-arytenoid muscle** consists of two portions, one external situated immediately within the ala of the thyroid cartilage, and one

Fig. 458.

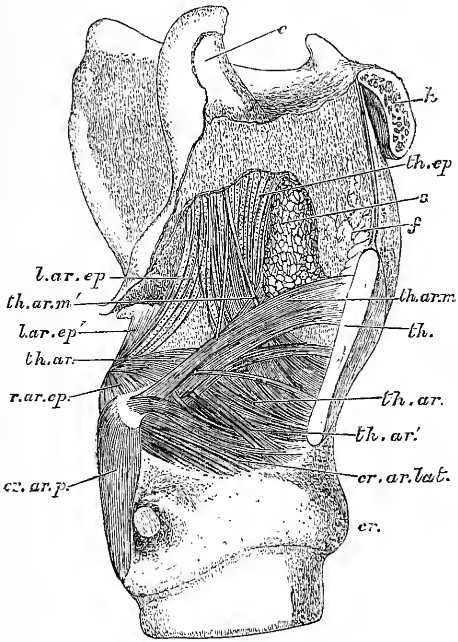


Fig. 458.—Side view of the larynx after removal of the right ala of the thyroid cartilage (S. G. Shattock).

h, body of hyoid bone, cut; *e*, epiglottis; *th*, cut surface of right ala of thyroid cartilage; *cr*, front of cricoid cartilage, the articular faces for the inferior corner of the thyroid is seen posteriorly; *th.ar*, *th.ar*, fibres of the thyro-arytenoid (outer portion) passing from the thyroid in front to the arytenoid behind; *th.ar'*, others arising from the crico-thyroid membrane; another considerable mass of fibres is seen arising from the same parts, and passing at first obliquely and afterwards nearly vertically upwards as the thyro-epiglottidean muscles, *th.ep.*; *th.ar.m*, small thyro-arytenoid; *th.ar.m'*, a small slip of the same muscle passing into the false vocal cord; *cr.ar.lat*, lateral crico-arytenoid; *cr.ar.p*, posterior crico-arytenoid; *r.ar.ep*, right aryteno-epiglottidean muscle near its origin; *l.ar.ep*, left aryteno-epiglottidean near its insertion; *l.ar.ep'*, portion of the same inserted into the corniculum; *f*, fat; *s*, saccule covered by mucous glands.

internal lying in close contact with the vocal cord. Sometimes these are described as distinct muscles under the names external and internal thyro-arytenoid (Henle), but the separation between them has generally to be effected by artificial means. The inner portion of the muscle is triangular in section corresponding with the vocal fold which it occupies; the outer is laterally compressed and extends both above and below the inner portion. Each contains both antero-posterior and oblique fibres.

Inner portion.—The antero-posterior fibres of the internal portion arise in the lower half of the angle formed by the alæ of the thyroid cartilage, a few even from a nodule of firmer elastic tissue (sometimes described as fibro-cartilage) in the anterior part of the vocal cord itself; and, passing backwards in a slight curve with the concavity inwards, are attached behind to the vocal process along its whole length and to the adjacent part of the outer surface of the arytenoid cartilage. They are joined internally by short fibres which are attached in front to the vocal cord, and behind to the vocal process of the arytenoid (*portio ary-vocalis* of Ludwig); and externally they are contiguous with the antero-posterior fibres of the external portion. The oblique fibres of the internal portion pass from the sloping portion of the crico-thyroid membrane below the vocal cord proper (in its anterior third), upwards, outwards, and somewhat backwards, passing between the antero-posterior fibres, and over the ventricle of Morgagni to end in the tissue of the false vocal fold.

Outer portion (fig. 458).—The fibres of the external portion arise in front from the thyroid cartilage close to the origin of the internal portion, and from the crico-thyroid membrane; from here they in part pass backwards to be inserted into the lateral border and muscular process of the arytenoid cartilage, in part obliquely upwards towards the aryteno-epiglottidean fold; some which are more vertical in direction passing in a thin layer around the ventricle of Morgagni and the sacculus to end in the false vocal fold. The portion of this muscle which extends towards the epiglottis is often described as a separate muscle under the name of **thyro-epiglottidean** (fig. 458, *th.ep*).

Action.—The bundles of the thyro-arytenoid muscle, differing as they do in direction and in points of attachment, must differ also in their action, if separately called into play. The antero-posterior fibres will tend to draw forwards the arytenoid, and with it the posterior part of the cricoid cartilage, rotating the latter upwards, and antagonising the action of the crico-thyroid, the effect being to relax the vocal cords. But if the latter be kept stretched and approximated by the action of other muscles, those fibres of the inner portion which are in close contact with the vocal cord may serve to modify its elasticity and consistence; while the fibres which constitute the portio ary-vocalis may serve, as Ludwig has pointed out, to tighten the parts of the cord in front of their attachment, and to slacken the parts behind. The vertical fibres of the muscle which extend from the sloping part of the crico-thyroid membrane across the base of the vocal fold, and over the ventricle into the false vocal cord, must, when they contract, render the free edge more prominent. Finally, the fibres which are inserted into the muscular process of the arytenoid will tend to rotate the vocal processes inwards, and those which pass up into the aryteno-epiglottidean folds may assist in depressing the epiglottis.

If the thyro-arytenoid muscles are paralysed, the lips of the glottis are no longer parallel, but are curved with the concavity towards one another, and a much stronger blast of air is required for the production of the voice.

Santorini described three thyro-arytenoid muscles, an *inferior*, a *middle*, and a *superior*. The latter is not always present. The inferior thyro-arytenoid muscle of Santorini comprises most of the antero-posterior bundles; the middle thyro-arytenoid, the oblique bundles of the external portion. The fibres of the superior fasciculus, when present, arise nearest to the notch of the thyroid cartilage, and are attached to the upper base of the arytenoid cartilage (fig. 458, *th.ar.m.*) This is named by Sœmmerring the *small* thyro-arytenoid whilst the two other portions of the muscle constitute the *great* thyro-arytenoid of that author.

When the mucous membrane is removed from the back of the arytenoid cartilages, a thick band of transverse fibres constituting the arytenoid

muscle is laid bare (fig. 456, 2), and on the surface of this are seen two slender decussating oblique bundles (3, 4), formerly described as portions of the arytenoid muscle (arytænoideus obliquus), but now more generally considered as parts of the aryteno-epiglottidean muscles, with which they are closely associated both in the disposition of their fibres and in their action. The **arytenoid muscle** (fig. 456, 2) passes straight across between the arytenoid cartilages, and its fibres are attached to the whole extent of the concave surface on the back of each. The **aryteno-epiglottidean** muscles (fig. 456, 5 ; fig. 458, *l.ar.ep*) arising near the inferior and outer angles of the arytenoid cartilages, decussate one with the other, and their fibres are partly attached to the upper and outer part of the opposite cartilage, partly pass forwards in the aryteno-epiglottic fold, and partly join the fibres of the thyro-arytenoid muscle.

Action.—The *arytenoid* muscle draws the arytenoid cartilages together, and, from the structure of the crico-arytenoid joints, this approximation when complete is necessarily accompanied with depression. If the muscle is paralysed, the intercartilaginous part of the glottis remains patent, although the membranous lips can still be approximated. The *aryteno-epiglottidean* muscles both approximate the arytenoid cartilages, which they include in their embrace, and draw down the epiglottis, so as to contract the whole superior aperture of the larynx.

Fig. 459.

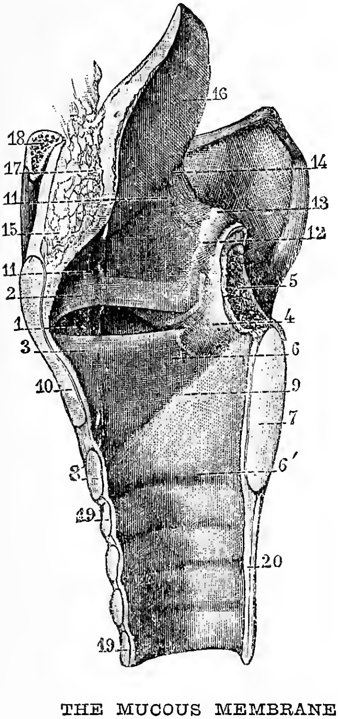


Fig. 459.—View of the interior of the right half of the larynx (Sappey).

1, ventricle ; 2, superior, and 3, inferior vocal cord ; 4, arytenoid cartilage covered by mucous membrane ; 5, arytenoid muscle cut across ; 6, slope of crico-thyroid membrane leading up to inferior vocal cord ; 6′, lower border of cricoid cartilage ; 7, 8, sections of cricoid ; 9, its upper border ; 10, section of thyroid ; 11, upper part of larynx ; 12, 13, glandular prominence in ary-epiglottidean fold ; 14, 16, epiglottis ; 15, fat between it and the thyro-hyoid membrane ; 17, section of epiglottis ; 18, section of hyoid bone ; 19, 20, trachea.

It is remarked by Henle that the muscles "which lie in the space enclosed by the laminæ of the thyroid cartilage, and above the cricoid, may be regarded in their totality as a kind of sphincter, such as is found in its simplest form embracing the entrance of the larynx in reptiles."

THE MUCOUS MEMBRANE AND VESSELS OF THE LARYNX.

The laryngeal **mucous membrane** is thin and of a pale colour. In some situations it adheres intimately to the subjacent parts, especially on the epiglottis, and still more in passing over the true vocal cords, on which it is very thin and most closely adherent. About the

upper part of the larynx, above the glottis, it is extremely sensitive. In and near the aryteno-epiglottic folds, it covers a quantity of loose areolar tissue, which is liable in disease to infiltration, constituting œdema of the glottis. Like the mucous membrane in the rest of the air-passages, that of the larynx is covered in the greater part of its extent with a columnar ciliated epithelium, by the vibratory action of which the mucus is urged upwards. The cilia are found higher up in front than on each side and behind, reaching in the former direction as high as the widest portion of the epiglottis, and in the other directions only to a line or two above the superior vocal cords; above these points the epithelium loses its cilia, and assumes a stratified squamous form, like that of the pharynx and mouth. Upon the true vocal cords also the epithelium is squamous, although both above and below them it is columnar and ciliated. Patches of stratified squamous epithelium are found also dotted here and there in the ciliated tract above the glottis, especially on the under surface of the epiglottis, the inner surface of the arytenoid cartilages, and at the free border of the superior vocal cord. Bodies which are to all appearance similar to the taste-buds presently to be described in the mucous membrane of the tongue are found imbedded in this stratified epithelium.

Fig. 460.

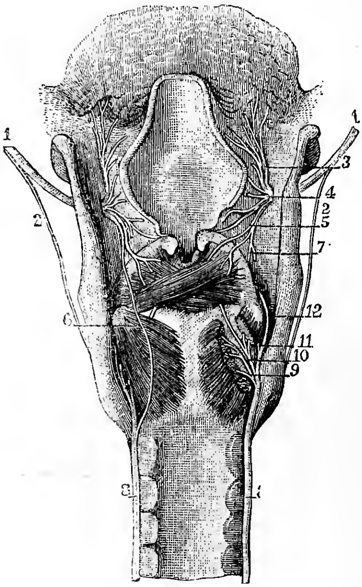


Fig. 460.—POSTERIOR VIEW OF THE NERVES OF THE LARYNX (SAPPEY).

1, superior laryngeal nerve; 2, its branch to the crico-thyroid muscle; 3, 4, 5, branches to the mucous membrane of the larynx; 6, filaments uniting the left superior and inferior laryngeal nerves; 7, the same on the right side, cut; 8, 8, inferior laryngeal nerves; 9, branch to the posterior crico-arytenoid muscles; 10, branch to the arytenoid; 11, 12, branches passing to the lateral crico-arytenoid and the thyro-arytenoid muscles.

The lining membrane of the larynx is provided with numerous *glands*, which secrete an abundant mucus; and the orifices of which may be seen almost everywhere, excepting upon and near the true vocal cords. They abound particularly upon the epiglottis, in the substance of which are found upwards of fifty small compound glands, some of them perforating the cartilage. Between the anterior surface of the epiglottis, the hyoid bone and the root of the tongue, is a mass of yellowish fat, erroneously named the epiglottic gland, in or upon which some small glands may exist. Another collection of glands is placed within the fold of mucous membrane in front of each arytenoid cartilage, from which a series may be traced forwards, along the corresponding superior vocal cord. The glands of the laryngeal pouches have already been noticed.

Vessels and Nerves of the Larynx.—The *arteries* of the larynx are derived from the superior thyroid, a branch of the external carotid, and from the inferior thyroid, a branch of the subclavian. The *veins* join the superior, middle, and inferior thyroid veins. The *lymphatics* are numerous, and pass through the cervical glands. Their mode of distribution resembles that in the trachea. The *nerves* are supplied from the superior laryngeal and inferior or recurrent laryngeal branches of the pneumogastric nerves, joined by branches of the sympathetic. The superior laryngeal nerves supply the mucous membrane, and the crico-thyroid muscles, and also in part the arytenoid muscle. The inferior laryngeal nerves supply, in part, the arytenoid muscle, and all the other muscles, excepting the crico-thyroid.

The superior and inferior laryngeal nerves of each side communicate with each other in two places, viz., at the back of the larynx, beneath the pharyngeal mucous membrane, and on the side of the larynx, under the ala of the thyroid cartilage. Numerous ganglion-cells are found on the branches, both on those which enter the muscles, and also underneath the mucous membrane. End-bulbs are also described in the mucous membrane which covers the posterior or laryngeal surface of the epiglottis (Lindemann).

The further details of the distribution of the vessels and nerves will be found in vol. 1.

Recent literature of the larynx.—*Luschka*, Der Kehlkopf des Menschen, Tübingen, 1871 ; *Jelenffy* in Pflüger's Archiv. VII., 1871, and Wiener med. Wochenschr, 1872 ; *Schech* in Zeitschr. f. Biol. IX., 1873 ; *Coyne* (mucous membrane) in Monthly Micro. Journal, 1874 ; *Heitler*, Aden. Subst. in d. Schleimhaut, Wiener med. Jahrb., 1874 ; *Rühlmann* (Muskeln) Wien. Sitzungsb., LXIX., 1874 ; *Disse*, Beiträge, &c., in Arch. f. mikr. Anat., XI., 1875 ; *Ziemssen*, Article "Diseases of respiratory apparatus" in his Handbook, 1876 ; *W. Gruber*, in Virch. Arch., LXVI., LXVII., 1876 ; St. Petersb. Memoires, XXIII., 1876 ; and Arch. f. Anat., 1875 and 1876 ; *Rüdinger*, Beiträge, &c., in Monatschr. f. Ohrenheilk., 1876 ; *Schofield*, in Journ. of Anat., 1876 (taste-buds in epiglottis) ; *Weinberg*, Gestalt d. Kehlkopf in versch. Lebensaltern, Arch. f. klin. Chirurg., 21, 1877 ; *Davis*, Die becherförm. Organe d. Kehlk., Arch. f. mikr. Anat. XIV., 1877 ; *Moura*, Dim. d. diverses parties d. lèvres vocales, Bull. de l'acad. de méd., 1879 ; *Grützner*, Article "Stimme u. Sprache" in Hermann's Handb. der Physiol., 1879 ; *S. G. Shattock*, in the Journal of Anatomy, 1882 (thyro-arytenoid muscle).

DUCTLESS GLANDS ON THE LARYNX AND TRACHEA.

THE THYROID BODY.

The **thyroid body** or **gland** (fig. 461) is a highly vascular organ, consisting of two *lateral lobes*, united together towards their lower ends by a transverse portion named the *isthmus*. Viewed as a whole, it is convex on the sides and in front, forming a rounded projection upon the trachea and larynx. It is covered by the sterno-hyoid, sterno-thyroid, and omo-hyoid muscles, and behind them it comes into contact with the sheath of the great vessels of the neck. Its deep surface is concave where it rests against the trachea and larynx. It usually extends so far back as to touch the lower portion of the pharynx, and on the left side the œsophagus also.

Each lobe extends from the fifth or sixth ring of the trachea to the side of the thyroid cartilage, of which it covers the inferior cornu and part of the ala near the posterior border.

The transverse part, or isthmus (*i*), commonly lies across the second, third, and fourth rings of the trachea, but is very inconstant in size, shape, and position. From the upper part of the isthmus, or from the adjacent portion of either lobe, a slender conical process, named the *pyramid*, or *middle lobe*, often proceeds upwards to the hyoid bone, to which its apex is attached by loose fibrous tissue.

This process usually lies somewhat to the left; occasionally it is thicker above than below, or is completely detached, or is split into two parts: sometimes it appears to consist of fibrous tissue only. In many cases muscular fasciculi, most frequently derived from the thyro-hyoid muscle, but occasionally independent, descend from the hyoid bone to the thyroid gland or its pyramidal process. They are known as the *levator glandulæ thyroideæ* (fig. 461, *lt*). It sometimes, though rarely, happens that the isthmus is altogether wanting, the lateral lobes being then connected by areolar or fibrous tissue only: this is the natural condition in some animals.

Each lateral lobe measures about two inches in length, an inch and a quarter in breadth, and three-quarters of an inch in thickness at its largest part, which is below its middle: the right lobe is usually a little longer and wider than the left.

The isthmus measures nearly half an inch in breadth, and from a quarter to three-quarters of an inch in depth.

The *weight* of the thyroid body is ordinarily from one to two ounces. It is always larger in females than in males, and appears in many of the former to undergo a periodical increase about the time of menstruation. It varies a good deal in size, and occasionally undergoes enormous enlargement. Its *colour* is usually of a dusky brownish red, but sometimes of a yellowish hue.

Fig. 461.

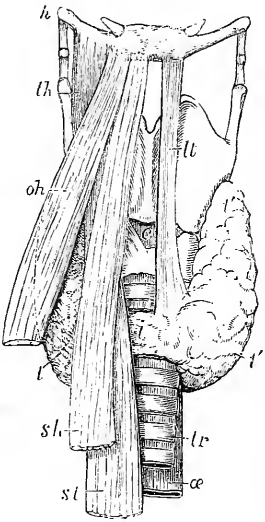


Fig. 461.—Sketch showing the form and position of the thyroid body (Allen Thomson). One-half the natural size.

The larynx and surrounding parts are viewed from before; on the right side the muscles covering the thyroid body are retained, on the left side they are removed; *h*, hyoid bone; *th*, right thyro-hyoid muscle; *o h*, omo-hyoid; *sh*, sterno-hyoid; *st*, sterno-thyroid; *c*, crico-thyroid membrane; *tr*, trachea; *œ*, œsophagus; *t*, right lobe of the thyroid body; *t'*, the left lobe; *i*, the isthmus; *lt*, the fibrous or muscular band termed levator thyroideæ, which is more rarely found in the middle line or to the right side, and which existed in the case from which the figure was taken.

Structure.—The texture of this organ is firm, and to the naked eye appears coarsely granular. It is invested by a thin transparent layer of dense areolar tissue, which connects it with the adjacent parts, and imperfectly separates its substance into small lobules of irregular form and size.

When the organ is cut into, a yellow glairy fluid escapes from the cut surface. Imbedded in its substance are multitudes of closed *vesicles* (fig. 462), which are held together in groups or imperfect lobules by areolar tissue. The size of the vesicles varies from $\frac{1}{850}$th of an inch to that of a millet-seed, so as to be visible to the naked eye. They are spherical, polyhedral, or flattened in shape. The wall of each vesicle consists of a simple layer of cubical or columnar epithelium-cells. According to Baber there is no basement membrane.

The vesicles may contain, besides the characteristic yellow glairy fluid (colloid), detached epithelium-cells, white blood-corpuscles, parenchyma-cells which seem to have migrated into the cavities, and also according to Baber red blood-corpuscles in various stages of disintegration and

decolourization. From this it is inferred that the thyroid body may be concerned in producing retrogressive changes in the blood.

In the interstitial connective tissue of the gland there occur a number of cells similar to the "plasma-cells" of Waldeyer ("parenchyma-cells," Baber). The spaces (areolæ) of this tissue may be filled with the same colloid substance as that which occupies the vesicles. The blood-vessels and lymphatics are conducted to the vesicles in the interstitial tissue, the

Fig. 462.

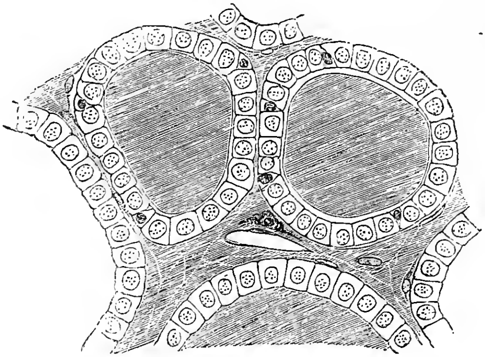


Fig. 462.—Section of the thyroid gland of a child (E.A.S.)

Two complete vesicles and portions of others are represented. The vesicles are filled with colloid which also occupies the interstitial spaces. In the middle of one of the spaces a blood-vessel is seen cut obliquely, and close to it is a plasma-cell. Between the cubical epithelium cells, smaller cells like lymph-corpuscles are seen here and there.

lymphatic vessels not coming into such intimate relations with the walls of the vesicles as the blood-capillary network, the vessels of which are in close contact with the epithelium and may even project between the epithelium-cells.

Although the vesicles are as a rule quite distinct from each other in the adult, incompletely developed portions may here and there be found in which anastomosing cylinders of columnar cells occur.

One of the most frequent pathological changes to which the thyroid body is subject consists in the accumulation within its vesicles of colloid substance: in certain forms of goître it distends them to an enormous degree.

In the fœtus, and during early infancy, this organ is relatively larger than in after-life; its proportion to the weight of the body in the new-born infant being that of 1 to 240 or 400, whilst at the end of three weeks it becomes only 1 to 1160, and in the adult 1 to 1800 (Krause). In advanced life the thyroid body is liable to become indurated, and frequently contains earthy deposit; its vesicles also attain a very large size.

Vessels and nerves.—The *arteries* of the thyroid body are the superior and inferior thyroids of each side, to which is sometimes added a fifth vessel, the *thyroidea ima*. The arteries are remarkable for their large relative size, and for their frequent and large anastomoses; they terminate in a capillary network upon the outside of the vesicles. The *veins*, which are also large, ultimately form plexuses on the surface, from which a superior, middle, and inferior thyroid vein are formed on each side. The superior and middle thyroid veins open into the internal jugular; the inferior veins issue from a plexus formed in front of the trachea, and open into the innominate veins. The *lymphatics* of the thyroid body form numerous and large anastomosing trunks, both at the surface of the

organ and throughout its substance; they originate, according to the observations of Frey, in the connective tissue which unites the gland-vesicles, with the cavity of which they appear not to be in communication. They contain, besides lymph, colloid substance, similar to that found within the vesicles (Baber).

The *nerves* are derived from the middle and inferior cervical ganglia of the sympathetic. They accompany the blood-vessels; and have here and there ganglion-cells in their course; their mode of ending is unknown.

Recent Literature.—*Peremeschko* in Zeitschr. f. wiss. Zool., 1867; *W. Müller* in Jena. Zeitschr., 1871; *Verson*, Article in Stricker's Handbook, 1871; *Boéchat*, Thesis, Paris, 1873; *Poincaré* in J. de l'anat., 1875; *Baber* in Phil. Trans., 1876 and 1881; *Zeiss*, Dissert., Strassburg, 1877; (on anatomical peculiarities of the thyroid) *W. Gruber* in Arch. f. Anat., 1876 and in Virch. Arch. LXVI., 1876; (on an accessory thyroid) *Marten* in Arch. f. Anat., 1879.

THE THYMUS GLAND.

The **thymus gland** or **body** is a temporary organ which reaches its greatest size at about the end of the second year of life, after which period it ceases to grow, and is gradually reduced to a mere vestige. Its function is not fully understood, although it is probable that it is in some way connected with the elaboration of the blood in infancy. When examined in its mature state in an infant under two years of age, it appears as a narrow elongated glandular-looking body, situated partly in the thorax, and partly in the lower region of the neck (fig. 463): below, it lies in the superior mediastinal space, close behind the sternum as far down as the fourth rib-cartilage, and in front of the great vessels and pericardium; above, it extends upwards upon the trachea in the neck as high as the lower border of the thyroid, being covered by the sterno-hyoid and sterno-thyroid muscles. Its colour is greyish, with a pinkish tinge; its consistence soft and pulpy, and its surface appears distinctly lobulated. It consists of two *lateral lobes*, which touch each other along the middle line, and are of a nearly symmetrical long pyramidal form, though generally unequal in size, sometimes the left, and at other times the right lobe being the larger of the two. An *intermediate lobe* often exists between the two lateral ones, and occasionally the whole body forms a single mass.

Externally the gland is in contact with the pleura, near the internal mammary artery, and higher up (in the neck), with the sheath of the carotid artery. The dimensions of the thymus vary according to its stage of development. At birth it measures rather more than two inches in length, an inch and a half in width at its lower part, and about one quarter or one third of an inch in thickness. Its weight at that period is about half an ounce.

At puberty the thymus is generally reduced to a mere vestige which has entirely lost its original structure, and consists of brownish tissue occupying part of the superior mediastinum. Occasionally it is still found in good condition at the twentieth year; but generally only traces of it remain at that time, and these are rarely discoverable beyond the twenty-fifth or thirtieth year.

Structure.—The lateral lobes of the thymus gland are each invested by a thin capsule of areolar tissue, which sends partitions into the gland between the lobules: on its outer surface the capsule is covered by a layer of flattened cells. Each lobe consists of numerous polyhedral *lobules*, connected by a more delicate intervening areolar tissue. These primary lobules are made up of a number of small nodules or follicles (fig. 464, *b*, *b*), one to two millimetres in diameter. Each follicle

is composed of a central part or *medulla*, and an external larger part or *cortex*. The cortex is in many respects similar in structure to an ordinary lymphoid follicle, such as those of the tonsils or of Peyer's patches in the intestine: consisting, like these, of retiform tissue composed of a network of branched cells, and of a fine *reticulum* (Watney), the meshes

Fig. 463.

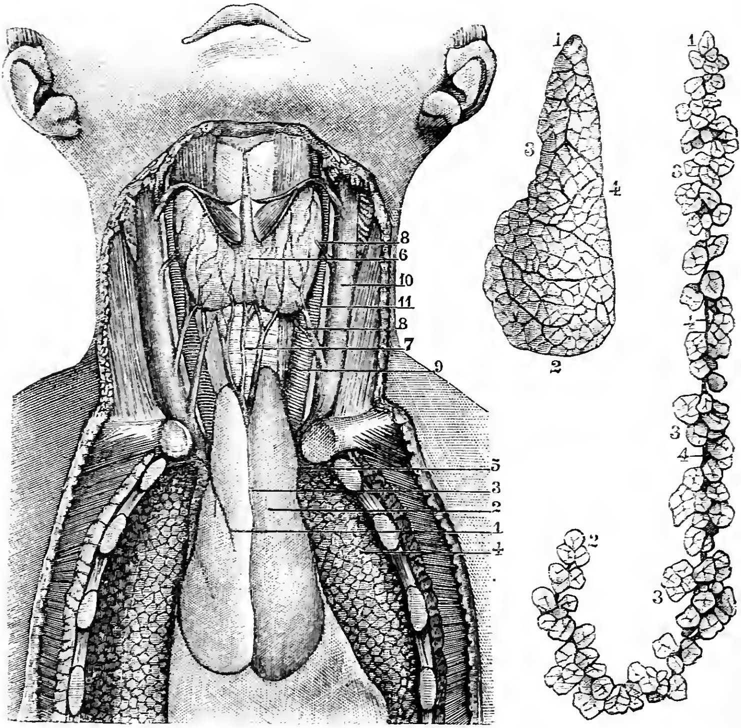


Fig. 463.—The thymus in a child of six months (Sappey).

A. Situation, form and relations of the gland. 1, right lobe; 2, left lobe; 3, median furrow; 4, lung, somewhat everted; 5, internal mammary vein; 6, thyroid body; 7, 8, inferior thyroid veins, mesial and lateral; 9, common carotid artery; 10, internal jugular vein; 11, pneumogastric nerve. B. Right lobe of the thymus after removal of its envelope; 1, its apex; 2, its base; 3, thin outer border; 4, thick inner border. C. The gland unravelled, showing the lobules grouped around a central cord; 4, the central cord or strand of connective tissue, connecting the lobules.

of both being filled with lymphoid cells (thymus corpuscles); at the surface of the follicle the retiform tissue is somewhat closer, so as to form a species of capsule for it. In some animals these capsules completely enclose the follicles, but in others, including man, several follicles may be united towards the centre of the lobule, which is then commonly of softer consistence than the other parts, and apt to break down if not perfectly fresh, so as to give the deceptive appearance of a central cavity (see fig. 464).

In the medulla, the retiform tissue is coarser and the lymphoid cells

fewer ; but it contains here and there peculiar corpuscles, which present an appearance of concentric striation, and are known as the *concentric corpuscles of Hassall.* They vary in size from that of a blood-corpuscle to three times that diameter, or more ; the larger often contain smaller ones in their interior.

Each is composed of an envelope of epithelioid cells enclosing a central mass, formed of one or more granular cells. The latter are also found, unenclosed, in the retiform tissue of the follicle, and occasionally attain a large size (giant-cells). The concentric corpuscles are often attached to blood-vessels and to each other by bands of fibrous tissue, and it has been inferred by Afanassiew that they are merely portions of vessels which have become atrophied, but according to Watney this is not the case ; since, at the time when they are most abundant, the formation of blood-vessels, and of blood-corpuscles within them, is proceeding most actively in the glands. Cysts, lined with ciliated epithelium, have been found by Watney in the thymus of the dog.

Fig. 464.

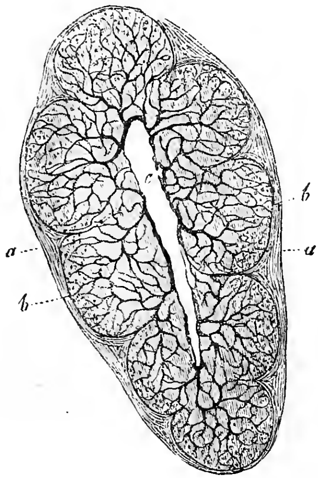


Fig. 464.—SECTION OF A LOBULE OF AN INJECTED INFANTILE THYMUS GLAND (from Kölliker). MAGNIFIED.

a, capsule of connective tissue surrounding the lobule ; *b*, *b*, follicles ; *c*, cleft in the centre of the lobule, probably produced by the shrinking away of the soft follicular substance.

The retrogressive development of the gland is accompanied by an increase in the interstitial connective tissue, which also invades the follicles. In this tissue plasma-cells become accumulated, and are eventually transformed into fat-cells, the normal structure of the thymus becoming gradually obliterated.

Vessels and Nerves.—The *arteries* of the thymus are derived from various sources, viz., from the internal mammary, the inferior and superior thyroid, the subclavian and carotid arteries. Their branches penetrate to the follicles, where they form a plexus which surrounds the cortex and from which capillaries converge towards the medulla. In some animals these vessels loop back towards the cortex, but in others they open into an inner vascular circle which lies just within the boundary of the medulla. The *veins*, for the most part, open into the left innominate vein.

The *lymphatics* are large. According to the observations of His on the calf, the larger blood-vessels passing to the centre are each accompanied by two or more lymphatic trunks. These arise from an interlobular plexus, which again is in connection with vessels which surround and enclose the individual follicles without penetrating them (as in those of the intestine).

The *nerves* are very minute. Haller thought that they were partly derived from the phrenic nerves, but according to Cooper, no filaments from these nerves go into the gland, although they reach the investing capsule, as does also a branch from the descendens noni. Small filaments, derived from the pneumogastric and sympathetic nerves, descend, on the thyroid body, to the upper part of the thymus. Sympathetic nerves also reach the gland along its various arteries.

For the **literature** of the thymus, as well as many details of its comparative structure, the reader is referred to a paper by Dr. H. Watney in the Phil. Trans. for 1882.

ORGANS OF DIGESTION.

The *digestive apparatus* consists of the *alimentary canal*, together with various glands of which it receives the secretions.

The alimentary canal commences at the mouth and terminates at the anus. Its average length is about thirty feet,—about five or six times the length of the body.

The part in the head and thorax consists of the *mouth*, with the *teeth*, and *salivary glands*, the *pharynx*, and the *œsophagus* or gullet. The part contained in the abdomen and pelvis consists of the *stomach* and the *small* and *large intestine*. Numerous small glands are situated in the mucous membrane of the alimentary canal, and the ducts of larger glands, the *salivary glands*, *pancreas* and *liver*, open on its inner surface.

THE MOUTH.

The **mouth** is bounded by the lips, cheeks, tongue, and the hard and soft palate, and communicates behind with the pharynx through the *fauces* (isthmus faucium). It is lined throughout by mucous membrane, and into it open the ducts of the salivary glands.

The *lips* and *cheeks* are composed externally of skin, and internally of mucous membrane, between which are included muscles, vessels, and nerves fully described in other parts of this work, areolar tissue, fat, and numerous small glands. The free border of the lips is protected by a dry mucous membrane, which becomes continuous with the skin, is covered with numerous minute vascular papillæ (fig. 465), and is highly sensitive. In some of these papillæ nerve end-bulbs, approaching in character to tactile corpuscles, are found. On the inner surface of each lip, the mucous membrane forms a fold in the middle line, connecting the lip with the gums. These are the *fræna* or *frænula:* that of the upper lip is the larger.

Fig. 465.

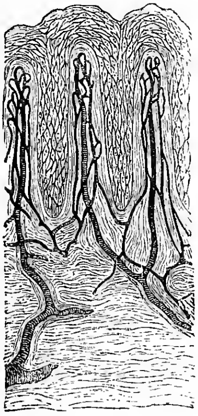


Fig. 465.—Three papillæ from the lip, with the blood-vessels injected (Toldt).

Numerous small racemose glands (*labial glands*) open on the inner surface of the lips near the oral aperture. They are situated between the mucous membrane and the orbicularis oris muscles.

Other small glands (*buccal glands*) lie between the buccinator muscle and the mucous membrane of the cheek. Two or three, larger than the rest, found between the masseter and buccinator muscles, and opening by separate ducts near the last molar teeth, are called the *molar glands*. The secretion of these glands is understood to be mucus; whether it has any of the specific properties of saliva is not known. Small sebaceous glands occur on the outer part of the red border of the lips.

Immediately within the lips and cheeks are the *dental arches*, consisting of the teeth, gums, and alveolar borders of the maxillæ. The *gums* (gingivæ) are composed of dense connective tissue, cohering very closely with the periosteum of the alveolar processes, and covered by a

red and highly vascular mucous membrane, which is smooth in its general surface, but is beset with fine papillæ in the immediate vicinity of the teeth.

The mucous membrane of the mouth is lined by scaly stratified epithelium, containing in the deeper layers numerous cells marked with ridges and spines, like those described in the epidermis.

THE TEETH.

In the human subject, as in mammalia generally, two sets of teeth make their appearance in the course of life, of which the first comprehends the *temporary* or *milk* teeth, whilst the second is the *permanent* set. The temporary teeth are twenty in number, ten in each jaw, and the permanent set consists of thirty-two, sixteen above and sixteen below.

GENERAL CHARACTERS OF THE TEETH.

A **tooth** consists of three portions, viz., one which projects above the gums and is named the body or *crown*, another fixed in the alveolus or socket, the *root*, consisting of a *fang* or *fangs*—and a third, intermediate between the other two, and, from being more or less constricted, named the *neck* (fig. 466). The size and form of each of these parts vary in the different kinds of teeth.

The roots of the teeth are accurately fitted to the alveoli of the jaws, in which they are implanted. Each alveolus is lined by periosteum (dental periosteum, fig. 466, 4), which also invests the contained tooth as high as the neck, and is blended above with the dense tissue of the gums. The fangs of all the teeth taper from the cervix to the point, and this form, together with the accurate adjustment to the alveolus, has the effect of distributing the pressure during use over the whole socket, and of preventing it from unduly bearing on the point of the fang, through which the blood-vessels and nerves enter.

The thirty-two permanent teeth consist of four incisors, two canines, four bicuspids, and six molars in each jaw. The twenty temporary teeth are four incisors, two canines, and four molars above and below. There are no bicuspids among the temporary teeth, the eight deciduous molars preceding eight bicuspids of the permanent set. The relative position and arrangement of the different kinds of teeth in the jaws may be expressed by the following formula, which also exhibits the relation between the two sets in these respects :—

		MO.	BI.	CA.	IN.	CA.	BI.	MO.		
Temporary teeth . . .	Upper	2		1	4	1		2	=10	=20
	Lower	2		1	4	1		2	=10	
Permanent teeth . . .	Upper	3	2	1	4	1	2	3	=16	=32
	Lower	3	2	1	4	1	2	3	=16	

THE PERMANENT TEETH.—The **incisors** (fig. 467), eight in number, are the four front teeth in each jaw, and are so named from being adapted for cutting or dividing the food. Their *crowns* are chisel-shaped (*c*), and have a sharp horizontal cutting edge, which by continued use is bevelled off behind in the upper teeth, but in the lower ones is worn down in front, where it comes into contact with the over-lapping edges of the upper teeth. Before being subjected to wear, the horizontal

edge of each incisor is marked by three small prominent points, separated by two slight notches (fig 467, *d*). The anterior surface of the crown is slightly convex, and the posterior concave. The *fang* is

Fig. 466.

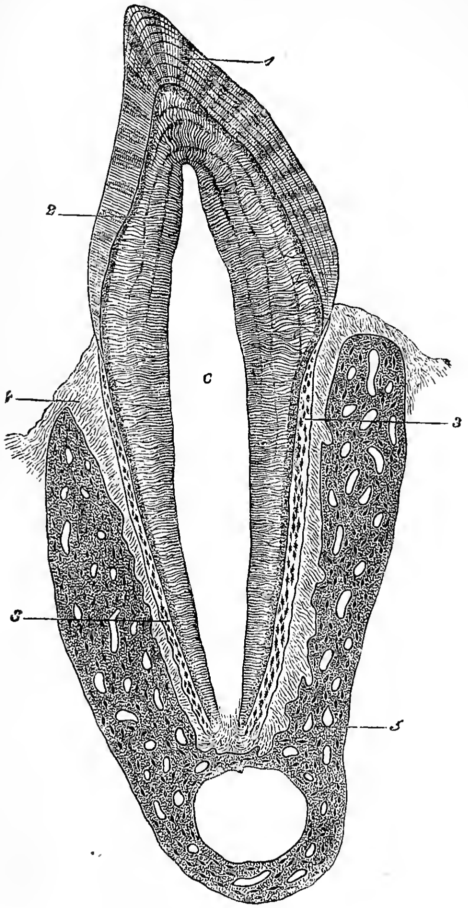


Fig. 466.—Vertical section of premolar of cat. 15 diameters (Waldeyer).

c, is placed in the pulp-cavity, opposite the cervix or neck of the tooth; the part above is the crown, that below is the root (fang). 1, enamel with radial and concentric markings; 2, dentine with tubules and incremental lines; 3, cement or crusta petrosa, with bone corpuscles; 4, dental periosteum; 5, bone of lower jaw.

long, single, conical, and compressed at the sides, where it sometimes though rarely presents a slight longitudinal furrow (as in *c*).

The lower incisor teeth are placed vertically in the jaw, but the corresponding upper teeth are directed obliquely forwards. The upper incisors are, on the whole, larger than the lower ones. Of those in the upper jaw the central incisors are the larger; but in the lower jaw, the central incisors are the smaller, and are, indeed, the smallest of all the incisor teeth.

The **canine** teeth (fig. 468), four in number, are placed one on each side, above and below, next to the lateral incisors. They are larger and stronger than the incisor teeth. The *crown* is thick and conical, convex in front and hollowed behind, and may be compared to that of a large incisor tooth the angles of which have been removed, so as to leave a single central point or *cusp*, whence the name *cuspidate* applied to these teeth. The point always becomes worn down by use. The *fang* of the canine teeth is single, conical, and compressed at the sides: it is longer than the fangs of any of the other teeth, and is so thick as to cause a prominence of the alveolar arch: on the sides it is marked by a groove, an indication, as it were, of the cleft or division which appears in the teeth next behind.

The upper canines, popularly called the *eye-teeth*, are larger than the lower, and in consequence of this, as well as of the greater width of the upper range of incisors, they are thrown a little farther outwards than the lower ones. In the dog-tribe, and in the carnivora generally, these teeth acquire a great size, and are fitted for seizing and killing prey, and for gnawing and tearing it when taken as food.

Fig. 467.

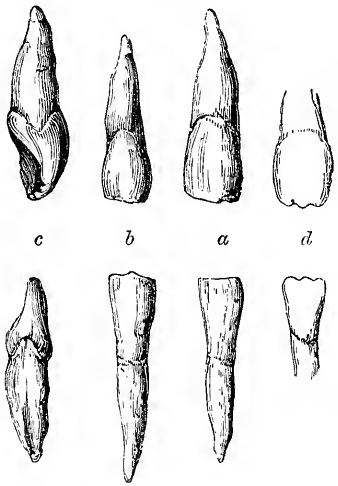


Fig. 467.—Incisor teeth of the upper and lower jaws.

a, front view of the upper and lower middle incisors; *b*, front view of the upper and lower lateral incisors; *c*, lateral view of the upper and lower middle incisors, showing the chisel shape of the crown; a groove is seen marking slightly the fang of the lower tooth; *d*, the upper and lower middle incisor teeth before they have been worn, showing the three points on the cutting edge.

The **bicuspids** (fig. 469), also called *premolars*, are four in each jaw; they are shorter and smaller than the canines, next to which they are placed. The *crown* is compressed antero-posteriorly, and is convex, not only on its outer or labial surface, like the preceding teeth, but on its inner surface also, which rises vertically from the gum; it is broader than that of an incisor or canine tooth, and is surmounted by *two* pointed tubercles or cusps, of which the external one is larger and higher than the other. The *fang* is similarly compressed, and is deeply grooved in all cases, showing a tendency to become double.

Fig. 468.

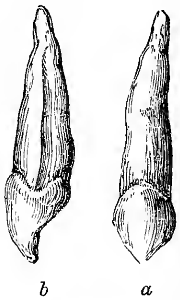


Fig. 468.—Canine tooth of the upper jaw.

a, front view; *b*, lateral view, showing the long fang grooved on the side.

The apex of the fang is generally bifid, and in the second upper bicuspid the root is often cleft for a considerable distance; but the bicuspid teeth are very variable in this respect, and may be, all four, free from any trace of bifidity of the root. The upper bicuspids are larger than the lower ones, and their cusps are more deeply divided. Sometimes the first lower bicuspid has only one tubercle distinctly marked, *i.e.*, the external, and in that case approaches in figure to a canine tooth.

The **molar** teeth (fig. 470), true or large molars, or *grinders*, are twelve in number, and are arranged behind the bicuspid teeth, three on each side, above and below. They are distinguished by the large size of the crown, and by the great width of its grinding surface. The first molar is the largest, and the third is the smallest, in each range, so as to produce a gradation of size in these teeth. The last of the range,

owing to its late appearance through the gum, is called the *wisdom-tooth.* The *crowns* of the molar teeth are low and cuboid in their general form. Their outer and inner surfaces are convex, but the crowns are rather flattened before and behind. The grinding surface is nearly square in the lower teeth, and rhomboidal in the upper, the corners being rounded off; it bears four or five trihedral tubercles or cusps (whence the name *multicuspidati*), separated from each other by a crucial depression.

Fig. 469.

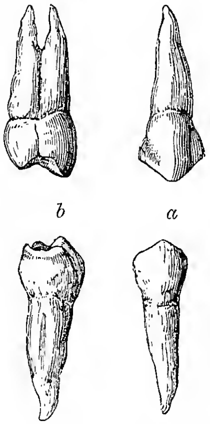


Fig. 470.

Fig. 469.—First bicuspid tooth of the upper and lower jaws.

a, front view; *b*, lateral view, showing the lateral groove of the fang, and the tendency in the upper to division.

Fig. 470.—First molar tooth of the upper and lower jaws.

They are viewed from the outer aspect.

The bicuspid and the molar teeth, from the breadth and uneven character of their masticating surface, are fitted for bruising, crushing, and grinding the food.

The *fangs* of the molar teeth are multiple. The upper molars have four cusps situated at the angles of the masticating surface; of these the anterior internal cusp is the largest, and is frequently connected with the posterior external cusp by a low oblique ridge. In the upper wisdom-teeth, the two internal cusps are usually blended. The crowns of the lower molars, which are larger than those of the upper, have five cusps, the additional one being placed between the two posterior ones, and rather to the outer side; this is especially evident in the lower wisdom-teeth, in which, however, the crown is smaller and rounder than in the others. In the two anterior molars of the *upper* jaw, the fangs are three in number, viz., two placed externally, which are short, divergent, and directed towards the antrum of the superior maxilla; and a third or internal fang, which is larger and longer, and is directed towards the palate, its posterior border extending as far back as that of the posterior external fang. This third fang is often slightly grooved, especially when the two internal cusps of the crown are very distinct, and sometimes it is divided into two smaller fangs. The two anterior molars of the *lower* jaw have each two broad, compressed fangs, one anterior, the other posterior, which are grooved on the faces that are turned towards each other, as if each consisted of two fangs fused together; they have

an inclination or curve backwards in the jaw, and are slightly divergent, but sometimes parallel, or even nearly in contact with each other; more rarely one or both of them is divided into two smaller fangs. In the wisdom-teeth of both jaws the fangs are often collected into a single irregular conical mass, which is either directed backwards in the substance of the jaw, or curved irregularly; this composite fang sometimes shows traces of subdivision, and there are occasionally two fangs in the lower tooth and three in the upper.

The range of teeth in each jaw forms a nearly uniform curve, which is not broken by any interval, as is the case in many mammals, and even in some of the Quadrumana. The upper dental arch is rather wider than the lower one, so that the teeth of the upper jaw slightly overhang those of the lower. While there is a slight diminution in the height of the crowns of the teeth from the incisors backwards to the wisdom-teeth, there is in man no abrupt change of level along the range. In consequence of the large proportionate breadth of the upper central incisors, the other teeth of the upper jaw are thrown somewhat outwards, so that in closure of the jaws the canines and bicuspids come into contact partly with the corresponding lower teeth, and partly with those next following; and in the case of the molars, each cusp of the upper lies behind the corresponding cusp of the lower teeth. Since, however, the upper molars and especially the wisdom-teeth are smaller than those below, the dental ranges terminate behind nearly at the same point in both jaws.

THE MILK-TEETH (fig. 471).—The temporary **incisor** and **canine** teeth resemble those of the permanent set in their general form; but they are of smaller dimensions. The temporary **molar** teeth present some peculiarities. The hinder

Fig. 471.

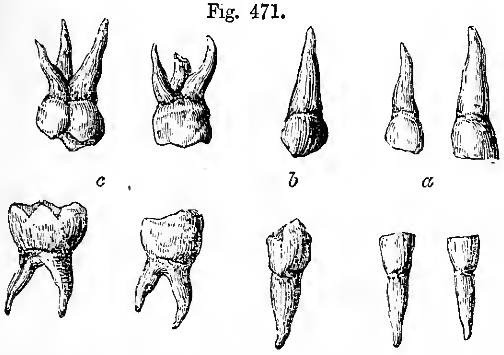


Fig. 471.—MILK TEETH OF THE RIGHT SIDE OF THE UPPER AND LOWER JAWS. *a*, the incisors; *b*, the canines; *c*, the molar teeth.

of the two is much the larger; it is the largest of all the milk-teeth, and is larger even than the second permanent bicuspid, which it afterwards gives place to. The first upper milk molar has only three cusps, two external and one internal; the second has four. The first lower temporary molar has four cusps, and the second five, of which in the latter case three are external. The *fangs* of the temporary molars resemble those of the permanent set, but they are smaller, and are more divergent from the neck of the tooth.

STRUCTURE OF THE TEETH.

On making a section of a tooth, it is found to be hollow within (fig. 472). The form of the cavity bears a general resemblence to that of the tooth itself; it occupies the interior of the crown, and extends along each fang, at the point of which it opens by a small orifice. In the incisor teeth the cavity is prolonged above into two fine canals, which proceed one to each corner of the crown; in the bicuspid and molar teeth it advances a short distance into each cusp. In the case of a root formed

by the blending of two or more fangs, each division has a separate canal prolonged to its apex.

Pulp of the teeth.—The central cavity of a tooth is called the *pulp-cavity,* because it is occupied by a soft, highly vascular, and sensitive substance, called the *dental pulp.* This pulp consists of jelly-like connective tissue containing cells, blood-vessels and nerves, and a few fine fibres. The cells are partly disseminated in the matrix, and partly form a stratum at the surface of the pulp, where they are elongated, somewhat like the cells of columnar epithelium (see fig. 484, *c*, p. 558). The superficial cells (*odontoblasts*) send processes into tubules in the dentine, to be afterwards noticed, of which more than one may come from the same cell. The filaments within the tubules were first noticed by J. Tomes. The arteries and nerves, which are derived from the internal maxillary and fifth pair respectively, enter by the aperture at the point of each fang. The vessels form a capillary network beneath the super-

Fig. 472.

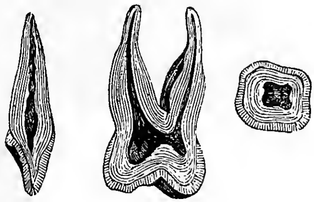


Fig. 472.—Sections of an incisor and molar tooth.

ficial cells; the nerves, as described by Boll in the rabbit's incisor, end in fine non-medullated fibres which are distributed abundantly at the surface of the pulp and run up between the superficial cells. Some appear to take the direction of those cell-processes which enter the hard tissue, but they have not with certainty been traced into the dentinal tubules.

According to Klein it is not the odontoblasts but other more deeply lying cells which send processes into the tubules of the dentine. To this it may be remarked that in the developing tooth it is not difficult to trace the filaments into the odontoblasts themselves.

Hard tissues of the teeth.—The hard part of a tooth is composed of three distinct substances,—viz., the proper dental substance, *ivory* or *dentine*, the *enamel*, and the *cement* or *crusta petrosa.* The dentine constitutes by far the larger portion; the enamel is found only upon the exposed part or crown; and the cement covers with a thin layer the surface of the fang.

The **dentine** (Owen,) resembles bone in its general aspect and chemical constitution, but is not identical with it in structure.

The dentine of human teeth is composed of 28 parts per cent. of animal, and 72 of earthy matter. The former is resolved into gelatin by boiling. The composition of the latter, according to Bibra, is as follows, viz., phosphate of lime 66·7 per cent., carbonate of lime 3·3, phosphate of magnesia and other salts, including a trace of fluoride of calcium, 1·8. Berzelius found 5·3 carbonate of lime.

The dentine is penetrated throughout by fine tubes, which being nearly parallel, give it a striated aspect (fig. 466). When a thin section is viewed under the microscope by transmitted light, the solid substance, or matrix, is transparent and apparently homogeneous, while the tubes, being (in a dried specimen) filled with air, are dark: but when seen with reflected light on a dark ground, the latter appear white; in these respects they resemble lacunæ and canaliculi of bone.

The *dentinal tubules* open at their inner ends into the pulp-cavity,

which presents very numerous minute orifices over the whole surface. Thence they pass in a radiated manner through every part of the ivory towards its periphery. In the upper part of the crown they have a vertical direction ; but towards the sides, and in the neck and root, they become gradually oblique, then horizontal, and are finally even inclined downwards towards the point of the fang. The tubules describe in their course two or three gentle curves (*primary* curvatures, fig. 466), and each is besides twisted throughout its whole length into numerous fine spiral turns, which follow more closely one upon another ; these are the *secondary* curvatures (fig. 473). In form a tubule may accordingly be

Fig. 473.

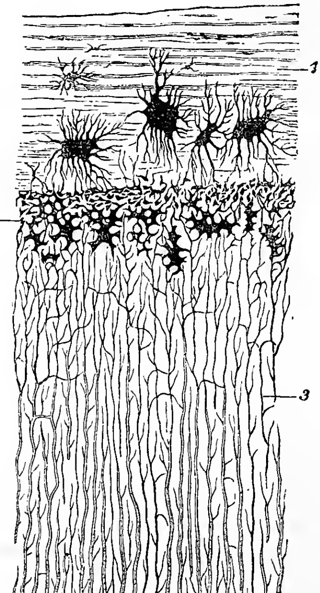


Fig. 473—SECTION OF FANG, PARALLEL TO THE DENTINAL TUBULES (HUMAN CANINE). MAGNIFIED 300 DIAMETERS. (Waldeyer.)

1, cement, with large bone-lacunæ and indications of lamellæ ; 2, granular layer of Purkinje (interglobular spaces) ; 3, dentinal tubules.

likened to the thread of a corkscrew, stretched so that the turns are drawn far apart, and their breadth proportionally diminished (Welcker).

The tubes are only slightly divergent as they pass towards the surface ; and, as they divide several times dichotomously, and at first without being much diminished in size, they continue to occupy the substance of the dentine at almost equal distances, and their nearly parallel primary curvatures produce, by the manner in which they reflect the light, an appearance of concentric undulations in the dentine, which may be well seen with a low magnifying power (*Schreger's lines*). The average diameter of the tubules at their inner and larger end is $\frac{1}{4500}$th of an inch, and the distance between adjacent tubules is commonly about two or three times their width. From their sides, numerous immeasurably fine branches are given off, which penetrate the hard intertubular substance, where they either anastomose or terminate blindly. These lateral ramuscles are more abundant in the fang. Near the periphery of the ivory the tubules, which by division and subdivision have become very fine, terminate imperceptibly by free ends.

The tubules have each a proper wall (*dentinal sheath*) independent of the intertubular matrix, but intimately adhering to it. By steeping sections of decalcified dentine in strong hydrochloric acid, the matrix is destroyed, and these membranous tubes, which consist of a more resisting material (probably elastic substance), remain behind.

In the temporary, and sometimes even in the permanent teeth, the tubules are constricted at short intervals, so as to present a moniliform character. The ter-

minal branches of tubules are occasionally seen to pass on into the cement which covers the fang, and to communicate with canaliculi proceeding from the characteristic lacunæ found in that osseous layer. Tubules have likewise been observed by Tomes passing into the enamel in the teeth of marsupial animals, and in a less marked degree, in human teeth.

Fig. 474.

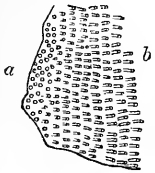


Fig. 474.—Sections of dentinal tubules (after Fraenkel).

a, cut across; *b*, cut obliquely. (About 300 diameters.)

The *intertubular substance* is translucent. The animal matter which remains, after the earth has been removed by an acid, may be torn into laminæ (Sharpey), parallel with the internal surface of the pulp-cavity, and therefore across the direction of the tubules. According to Ebner the matrix contains fine fibrils like those of the matrix of bone.

The laminated structure is an indication of the deposition of dentinal substance in successive strata in the process of formation of the tooth—the laminæ corresponding with the shape of the pulp-surface at successive stages of the process. Not unfrequently lines, varying in number and breadth, are seen in sections of the dry tooth, conforming in direction with the lamination just spoken of (*incremental lines*, Salter, fig. 475, *c*). They are caused by the drying of imperfectly calcified dentine, which shows little cavities bounded by, and therefore receiving their figure from, minute nodules or globules of dentine, and hence named *interglobular spaces* (fig. 476, *c*). The interglobular spaces, and the globules sur-

Fig. 475.

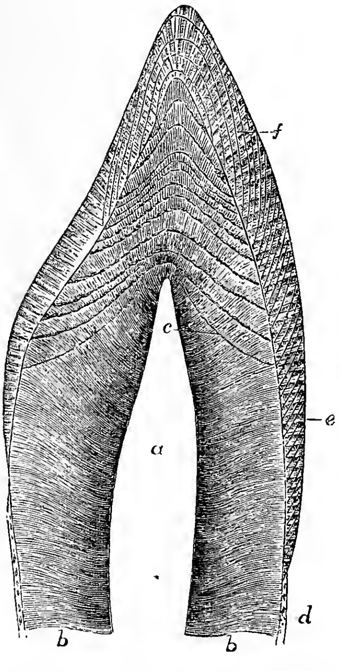


Fig. 475.—Vertical section of the upper part of an incisor tooth (from Kölliker) magnified 7 diameters.

a, the pulp-cavity; *b*, dentine; *c*, arched incremental lines; *d*, cement; *e*, enamel with bands indicating the direction of the ranges of fibres; *f*, coloured lines of the enamel.

Fig. 476.

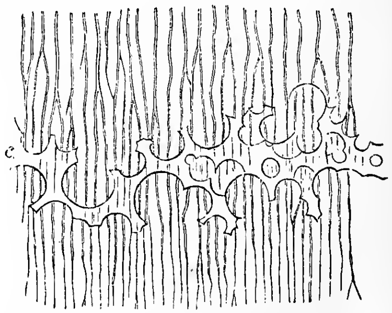


Fig. 476.—A small portion of the dentine with interglobular spaces (from Kölliker). 350 diameters.

c, portion of incremental line formed by the interglobular spaces, which are here filled up by the transparent material used in mounting the specimen.

rounding them, vary in size within wide limits. A layer, in which they are very fine—*granular layer* (fig. 473, 2)—is not uncommonly found towards the outer surface of the dentine.

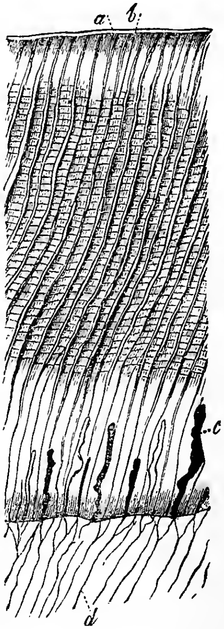
The **enamel** is that hard white covering which encrusts and protects the exposed portion or crown of a tooth. It is the hardest of all the dental tissues, but is gradually worn down by protracted use. It is thickest on the grinding surface and cutting edge of the teeth, and becomes gradually thinner towards the neck, where it ceases.

According to Bibra, it contains of earthy constituents 96·5 per cent., viz., phosphate of lime with traces of fluoride of calcium 89·8, carbonate of lime 4·4, phosphate of magnesia and other salts 1·3, and of animal matter only 3·5 per cent. Berzelius, however, gives the proportion of carbonate of lime as 8, and of animal matter as only 2 per cent..

Fig. 477.—Thin section of the enamel and a part of the dentine (from Kolliker). 350 diameters.

a, cuticular pellicle of the enamel; *b*, enamel-fibres or columns with fissures between them and cross striæ; *c*, clefts in the enamel communicating with the extremities of some of the tubuli (*d*).

Fig. 477.



The enamel is made up entirely of very hard and dense microscopic columns or prisms, arranged closely together, side by side, and set by one extremity upon the subjacent surface of the dentine (fig. 477). The columns are disposed in ranges which, on the grinding surface, are set vertically, but on the sides of the crown get more horizontal. Near the dentine the prisms cross one another in the alternate ranges, but become parallel as they approach the surface of the tooth; from this intercrossing the effect of radial alternate light and dark stripes is obtained (as in figs. 466 and 475). A series of concentric lines is likewise to be seen crossing the enamel fibres: these are termed *coloured lines* from their brown appearance, but whether caused by pigmentary deposit or otherwise is unascertained. Minute fissures not unfrequently exist in the deep part of the enamel, which run between clusters of the prisms down to the surface of the dentine (fig. 477, *c*); and other much larger and more evident fissures are often observed leading down from the depressions or crevices between the cusps of the molar and premolar teeth. The unworn surface of the enamel is finely striated.

The *enamel-columns* (fig. 478) have the form of solid six-sided prisms. Their diameter is ordinarily about $\frac{1}{5000}$th of an inch. They are marked by alternate dark and light transverse shadings, which are believed to be due to the existence of shallow constrictions along the fibres. The inner ends of the prisms are implanted in minute hexagonal depressions found on the surface of the dentine; whilst the outer ends are free, and present, when examined with a high magnifying power, a tesselated appearance (fig. 478, B). The prisms are united by a small

amount of a substance which appears similar to the intercellular substance of an epithelium, but is probably calcified. In the outer part of the enamel there are some shorter prisms interpolated between the others.

When submitted to the action of dilute acids, the enamel is almost entirely dissolved, and leaves scarcely any discernible traces of animal matter. The centre of the prisms is first dissolved, showing this part to be less firmly calcified than the periphery. By the action of an acid, the enamel of newly formed or still growing teeth may be broken up, and its structural elements more easily distinguished.

Fig. 478.

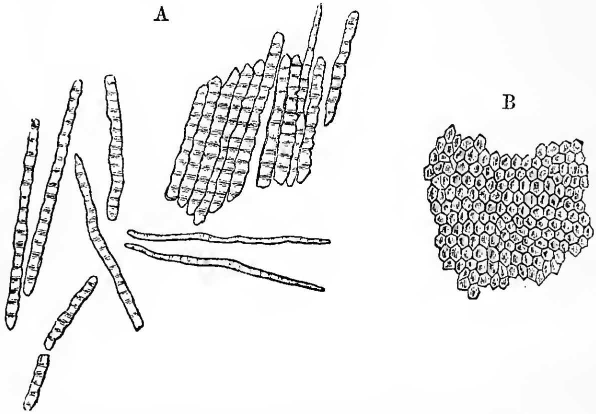


Fig. 478.—Enamel-prisms (from Kölliker). 350 diameters.

A, fragments and single columns of the enamel, isolated by the action of hydrochloric acid. B, surface of a small fragment of enamel, showing the hexagonal ends of the prisms.

It is further found, on treatment with acid, that a very thin membrane (*enamel cuticle*) entirely covers the enamel of unworn teeth upon its outer surface (fig. 477, *a*). This membrane forms a protective covering to the enamel. It is of an epithelial and horny nature, and withstands prolonged boiling as well as the action of acids and other re-agents. According to Tomes, this membrane is rather of the nature of cement, but without lacunæ. On this supposition, however, it is difficult to understand the meaning of the epithelial markings which are produced in it after the action of nitrate of silver.

The **crusta petrosa or cement** is the third substance which enters into the formation of the teeth. This is a layer of true bone, slightly modified in structure, and investing that part of the dentine which is not protected by the enamel. It covers the whole fang, towards the lower end of which it becomes gradually thicker, and is specially developed at the apex, and along the grooves of the compound fangs. As life advances, the cement generally grows thicker, especially near the point of the fang, where it sometimes blocks up the orifice leading to the pulp-cavity.

The crusta petrosa is lamellar in structure, and contains lacunæ and canaliculi resembling those of bone but larger and more irregular (fig. 473, 1). Where the cement is very thick it may contain Haversian canals. On the milk teeth the cement is thinner, and contains fewer cells. Perforating and decussating fibres, similar to those of ordinary bone, occur in the cement.

FORMATION OF THE TEETH.

A tooth is formed on the same fundamental type of development as a hair. In the latter case a process grows down from the Malpighian layer of the epidermis into the subjacent cutaneous corium, in which a depression is simultaneously produced for its reception. A papilla, soon becoming vascular, rises up from the bottom of the depression into the cellular mass, and the primitive tissue forming the wall of the recess is converted into the coats of a follicle. In the formation of a tooth there is in like manner a downgrowth from the Malpighian layer of the oral epithelium (which corresponds with the epidermis and is derived from the same embryonic layer). The cellular process is received into a recess of the subjacent mucous membrane. In this also a vascular papilla grows up from the bottom, and the simple wall of the cavity is differentiated into a vascular sac or follicle.

The first recognized steps in the development of the teeth take place as early as the seventh week of intra-uterine life. At this time the oral epithelium becomes thickened along the border of the jaws, and its Malpighian layer grows down into a corresponding groove, which is formed to receive it in the soft embryonic tissue of which the jaw then consists. The groove, although filled and covered in by the epithelium, is still faintly indicated by a shallow superficial furrow. This downgrowth of epithelium, which is named the "enamel-germ," forms the foundation of the special structures or organs which generate the enamel in the several teeth, and for the sake of distinction may be termed the **common enamel-germ** (fig. 479, 1). The groove, as well as the changes subsequently occurring in it, was observed by F. Arnold and by Goodsir, who named it the

Fig. 479.

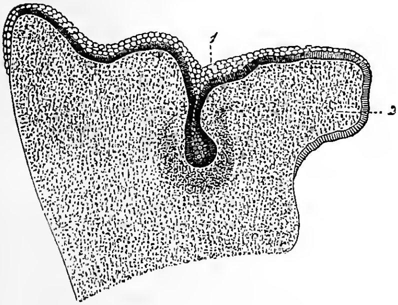


Fig. 480.

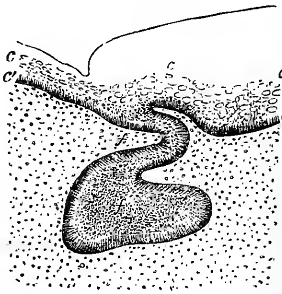


Fig. 479.—Section across the upper jaw of a fœtal sheep, 3 centimeters long. (from Waldeyer). $\frac{50}{1}$

1, common enamel-germ dipping down into the mucous membrane where it is half surrounded by a semilunar-shaped more dense-looking tissue, the germ of the dentine and dental sac ; 2, palatine process of the maxilla.

Fig. 480.—Section similar to that shown in the previous figure, but passing through one of the special enamel-germs here becoming flask-shaped (from Kölliker).

c, *c'*, epithelium of mouth ; *f*, neck ; *f'* body of special enamel-germ.

"primitive dental groove," but neither of these observers appears to have noticed the contained epithelium (or at least to have recognized its importance), probably in consequence of its soft and friable substance having been accidentally wiped away. The common enamel-germ, simultaneously with the groove, next increases in depth, and, at the same time, its deeper portion inclines outwards, forming an angle with its more superficial part. It also swells out below, so that a transverse vertical section of it is club or flask-shaped. An increased development then takes place at particular points, corresponding in situation with the ten milk-teeth ; and the common enamel-germ thus becomes parted in

its deeper portion, or extended by further growth, into as many distinct aggregations of cells, or **special enamel-germs**,—one for each tooth—of a club or flask-shape, connected by a narrowed neck with what remains of the common epithelial ingrowth (fig. 480, *f′*). These tooth-germs, as they may now be called, are lodged each in its own recess, which at this time is merely a pit in the soft embryonic tissue, without the membranous coats which afterwards are formed. From the bottom a **papilla** (fig. 481, *p*) meanwhile rises, soon becoming vascular, and assuming the shape of the future tooth-crown. It is received into a corresponding dimple of the enamel-germ, which now comes to resemble in form an inverted cup, and fits upon the papilla (fig. 481, A, *f′*).

Fig. 481.

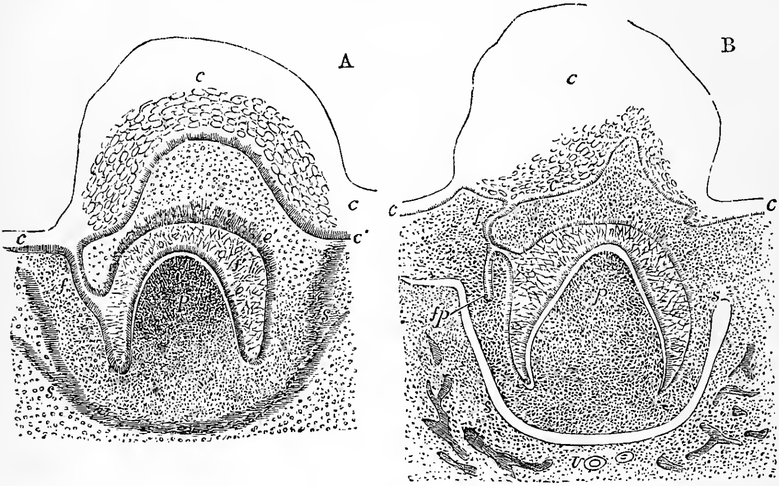


Fig. 481.—Sections at later stages than fig. 480 the papilla having become formed and indented the enamel-germ, which has at the same time grown partly round it. (from Kölliker).

c, epithelium of gum, sketched in outline, *f*, neck of enamel-germ, *f′*, enamel-organ ; *e*, its deeper columnar cells ; *e′*, projections into the corium ; *p*, papilla ; *s*, dental sac forming In B, the enamel-germ, *fp* of the corresponding permanent tooth has become formed.

The included enamel-germ is next cut off from connection with the superjacent epithelium, by obliteration of the neck of communication.

According to Goodsir the order in which the papillæ become distinct is very regular. That of the anterior milk molar is the first (7th week) ; that of the canine next (8th week) ; the incisor papillæ next (9th week), the central before the lateral ; and that of the posterior milk molar last (10th week). The several papillæ of the upper jaw appear a little earlier than the corresponding ones of the lower. About the sixteenth week there grows downwards and backwards from the narrow neck of each follicle, an epithelial bud, soon becoming elongated and swelling out at the bottom into a flask-shape. These are the germs of the ten anterior permanent teeth as will be afterwards shown.

While the above described changes are going on, the soft embryonic tissue bounding the depression which contains the enamel-germ, becomes converted into a vascular membranous sac (*dental sac*). This originates from a part of the same somewhat dense submucous tissue that gives rise to the dental papilla (see fig. 479), and the whole is supported by the osseous maxilla as soon as this is developed. The jaw is at first in the form of a bony gutter, in which the teeth-rudiments are lodged ; but this is soon divided by osseous partitions into chambers for the

several tooth-sacs, at first with wide openings, which afterwards are narrowed, but so as to allow the contained sacs to cohere with the gum along the border of the jaw. The alveoli are formed subsequently around the fangs of the teeth as these become developed, and the jaw is deepened by the growth of its alveolar border.

The **dental sacs** are well seen in the jaw of an infant a few months old, before the eruption of the teeth. They are represented at this stage in fig. 482. They consist of an outer fibro-vascular coat connected with the periosteum, and an inner highly vascular layer with a little jelly-like tissue interposed between the two. The inner coat is lined with the epithelium of the enamel organ to be hereafter described. Their blood-vessels are derived partly from the dental arteries which course along the base of the sacs, and partly from those of the gums. Their extreme vascularity doubtless has relation to the nutrition of the enamel organ.

Fig. 482.

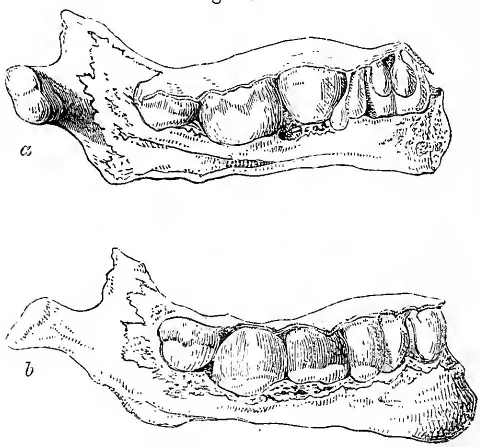


Fig. 482.—The dental sacs exposed in the jaw of a child at birth.

a, the left half seen from the inner side; *b*, the right half seen from the outer side; part of the bone has been removed so as to expose the dental sacs as they lie below the gum; the lower figure shows the sacs of the milk-teeth and the first permanent molar, exposed by removing the bone from the outside; the upper figure shows the same from the inside, together with the sacs of the permanent incisor and canine teeth adhering to the gum

The papillæ, now become the dental pulps, acquire a perfect resemblance to the crowns of the future teeth, and then the formation of the hard substance commences in them, as will be immediately described. This process begins very early, and by the end of the fourth month of fœtal life thin shells or caps of dentine (fig. 483) are found on all the pulps of the milk-teeth, and a little later on that of the first permanent molar, while at the same time the coating of enamel begins to be deposited on each.

The cap of dentine increases in extent by a growth around its edges, and in

Fig. 483.

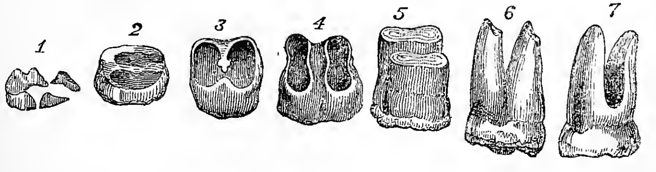


Fig. 483.—Different stages in the formation of an upper molar tooth with two fangs (from Blake).

1, the distinct caps of dentine for five cusps in the earliest stage of formation; in 2, and the remaining figures, the crown is downwards; in 2, and 3, the formation of the crown having proceeded as far as the neck, a bridge of dentine stretches across the base of the tooth-pulp; and in 4, the division of the fangs is thus completed; in 5, 6, and 7, the extension takes place in the fangs.

thickness by additions in its interior, while the substance of the pulp decreases in proportion. This growth of the tooth continues until the crown is completed of its proper width, and then the pulp undergoes a constriction at its base to form the cervix of the tooth, and afterwards elongates and becomes narrower, so as to serve as the basis of the fang. Sooner or later, after the completion of the crown, this part of the tooth appears through the gum, whilst the growth of dentine to complete the fang is continued at the surface of the elongating pulp, which gradually becomes encroached upon by successive formations of hard substance, until only a small cavity is left in the centre of the tooth, containing nothing but the reduced pulp, supplied by slender threads of vessels and nerves, which enter by a small aperture left at the point of the fang after the dentine is completed. In the case of teeth having complex crowns and more than a single fang, the process is somewhat modified. On the surface of the dental pulp of such a tooth, as many separate caps or shells of dental substance are formed as there are eminences or points; these soon coalesce, and the formation of the tooth proceeds as before as far as the cervix. The pulp then becomes divided into two or more portions, corresponding with the future fangs, and the ossification advances in each as it does in a single fang; while, at the same time, a horizontal projection or bridge of dentine is deposited across the base of the pulp, between the commencing fangs, so that if the tooth be removed at this stage and examined on its under surface, its shell presents as many apertures as there are separate fangs (fig. 483, 3 and 4). In all teeth, the pulp originally adheres by its entire base to the bottom of the sac; but, when more than one fang is to be developed, the pulp is, as it were, separated from the sac in certain parts, so that it comes to adhere at two or three insulated spots only, corresponding with the fangs, whilst the dentine continues to be formed along the surrounding free surface of the pulp.

Formation of the hard tissues of the Teeth.—The account already given of the structure of the permanent pulp of a tooth will apply also to that of the papilla or formative pulp of the growing tooth, both before and after the dentine

Fig. 484.

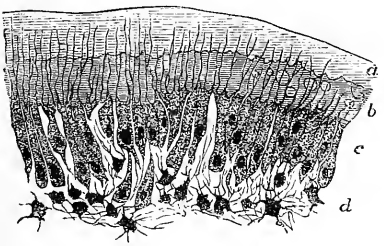


Fig. 484.—Part of section of developing tooth of a young rat, showing the mode of deposition of the dentine. Highly magnified. (E.A.S.)

a, outer layer of fully formed dentine; *b*, uncalcified matrix, with one or two nodules of calcareous matter near the calcified part; *c*, odontoblasts sending processes into the dentine; *d*, pulp. The section is stained with carmine, which colours the uncalcified matrix, but not the calcified part.

has begun to be formed from it. The capillary vessels, which form a series of loops a short distance beneath the surface, are much more abundant opposite the point or points where calcification is about to commence.

The **dentine** is produced more immediately by the elongated cells (odontoblasts) already described as forming the superficial stratum of the pulp (fig. 484, *c*). These cells send out from their free extremities filamentous processes, as described by Lent, and the matrix or intertubular substance of the dentine, which is probably shed out by the odontoblasts, becomes formed simultaneously between and around these processes and is thus as it were moulded upon them, so as to form the tubules in which the cell-processes are now enclosed. The same cell may continue to spin out a filament until the tubule is completed in its whole length, and in many cases a cell sends out two or more processes, coalescing into one as the cell recedes, the branched tubules being thus produced.

The collogenous basis of the dentinal matrix is at first uncalcified (fig. 484, *b*), but the material of calcification soon begins to be deposited in nodules or globules,

which run together into a uniform hard substance (*a*). In parts where this coalescence partially fails the uncalcified matter between the globules shrinks up when the tooth has become dry, so as to leave the interglobular spaces previously described (p. 552). The globular mode of deposition is indicated also by the inner surface of the growing dentine, which is nodulated (Czermak); and, indeed, separate nodules may be seen in the soft tissue of the growing matrix (see fig. 484, *b*).

Fig. 485.

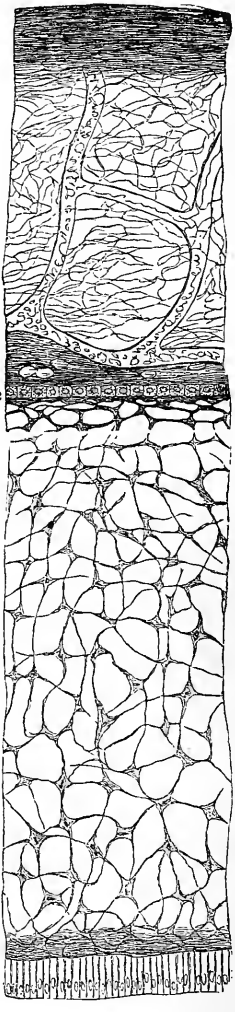


Fig. 485.—A SECTION THROUGH THE ENAMEL ORGAN AND DENTAL SAC FROM THE TOOTH OF A CHILD AT BIRTH (from Kölliker). 250 DIAMETERS.

a, outer dense layer of the dental sac; *b*, inner looser texture of the same with capillary blood-vessels and a somewhat denser layer towards the enamel organ; *c*, spongy substance; *d*, inner columnar cells; and *e*, outer cubical cells of the enamel organ.

[According to Waldeyer the protoplasm of the cells becomes directly transformed into the dentinal matrix, except the central part, which remains unaltered, occupying the tubule, and is prolonged by another cell lying deeper in the pulp, with which the first is in connection, and so on in succession. This view has been supported by Beale, Boll, Tomes, Klein, and other authorities, but in my opinion it is scarcely tenable. For if it were true we should expect to find odontoblasts which had only partly undergone the transformation in question, and such cells have never been described. We should further expect to find in the matrix vestiges of its coalesced formative cells, but these again have never been discovered in it. It is moreover very difficult to explain the branching of the tubules if we accept Waldeyer's view. Indeed this hypothesis seems to be based (like the similar views with regard to the formation of connective tissue and bone, see pp. 71-2 and 104-5) largely upon theoretical considerations, and to be opposed rather than supported by the known facts of the case (E. A. S.)]

The Enamel.—The surface cells of the enamel-germ line the dental sac in the form of a tesselated or cubical epithelium (fig. 485, *e*). On the other hand the cells which lie next the surface of the pulp become elongated and attenuated into a prismatic shape, precisely like a columnar epithelium (*d* fig. 485). The central cells undergo a remarkable change. Originally spheroidal, they for a time merely increase in number, but soon, assuming a stellate form, they send out branches which join with one another (fig. 485, *c*), whilst a clear fluid or jelly-like matter collects in their interstices.

Into the cavity containing the enamel-germ numerous small papillary processes of the vascular sac and adjacent mucous membrane project, and between these, on the other hand, epithelial processes extend from the enamel-germ into the membrane (fig. 486, 3). The enamel-germ is now designated the "enamel organ," *organon adamantinæ* of Purkinje, who named the columnar

epithelium on the surface of the pulp the *membrana adamantinæ*, or "enamel-membrane."

The enamel-prisms appear to be formed by the columnar cells of the enamel-organ, either by direct calcification of their substance or by deposition ; probably the former, since cells partly converted into hard substance have been observed by

Fig. 486.

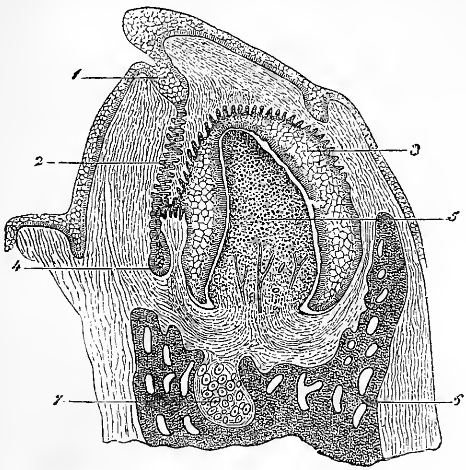


Fig. 486.—Section through the lower jaw of a human fœtus, 11 centimeters long (from Waldeyer). $\frac{25}{1}$

1, dental groove, occupied by epithelium continuous with that lining the mouth ; 2, remainder of the neck of the enamel-germ ; 3, enamel-organ ; papilliform projections are seen extending into it from the upper part of the dental sac ; 4, enamel germ of the corresponding permanent tooth : the space in which it is enclosed forms Goodsir's cavity of reserve ; 5, dentine-papilla ; 6, lower jaw-bone ; 7, Meckel's cartilage.

C. Tomes. The cells meanwhile may be supposed to grow continually at the other end. In sections a space is observed between the cells and the newly-formed enamel, but this is probably produced after death by a shrinking of the soft parts. The process of formation commences next to the forming dentine, almost as soon indeed as the latter begins to be produced. The enamel substance is at first soft and friable. The enamel-organ extends no farther than the crown of the tooth, to which, therefore, the deposit of enamel is limited. As the formation of enamel becomes completed the rest of the enamel-organ dwindles away : the superficial tesselated layer is believed to become the "cuticula dentis."

The **cement** begins to be formed, simultaneously with or soon after the dentine of the fang, by the subperiosteal tissue, as in the formation of the superficial layers of a bone.

Eruption of the temporary Teeth.—At the time of birth the crowns of the anterior milk-teeth, still enclosed in their sacs, lie in bony crypts in the jaw, with somewhat narrowed mouths opening on its edge. Their appearance through the gums follow a regular order, but the period at which each pair of teeth is cut varies within certain limits. The eruption commences about the age of seven months, and is completed about the end of the second year. It begins with the central incisors of the lower jaw (about the sixth to the ninth month), which are followed, after a resting period of two or three months, by the incisors of the upper jaw. Then after a rest of a few months come the lower lateral incisors and the first molars ; then after four or five months the canines, and finally about the second year the second molars.

The eruption of the tooth is preceded by absorption of part of the wall of the bony cavity in which it lies, especially of the front part, so as to leave a wide aperture for the emergence of the crown. After this a redeposition occurs around the neck of the tooth, and this deposition is continued around the fangs as these are becoming formed ; in this way the bony socket is produced.

Before the teeth protrude through the gum, this undergoes some peculiar changes : its edge at first becomes dense and sharp, but, as the tooth approaches it, the sharp edge disappears, the gum becomes rounded or tumid, and is of a

purplish hue; the summit of the tooth is seen like a white spot or line through the vascular gum, and soon afterwards emerges. Before the eruption, the mucous membrane is studded with a number of small white bodies, which were described by Serres as glands (*dental glands*). They are little nests of epithelium-cells (Sharpey) and appear to be portions of the epithelium of the enamel-germ which had escaped obliteration. Similar bodies are found in other situations where epithelium is included in a seam, and is undergoing obliteration, as along the line of closure of the palate (Epstein).

Development of the permanent Teeth.—Ten permanent teeth in each jaw succeed the milk-teeth, and six are superadded further back in the jaw. It will be convenient to treat first of the ten anterior teeth or *teeth of succession.*

The sacs and pulps of these teeth have their foundations laid before birth behind those of the milk set. It will be remembered that behind each milk-follicle there is formed about the sixteenth week a small epithelial growth (fig. 481, B, *fp*; fig. 486, 4), derived from the neck of the enamel-germ, and this forms the enamel-germ of the corresponding permanent tooth. They are ten in number in each jaw, and are formed successively from before backwards. These germs soon elongate and recede into the substance of the gum behind the germs of the

Fig. 487.

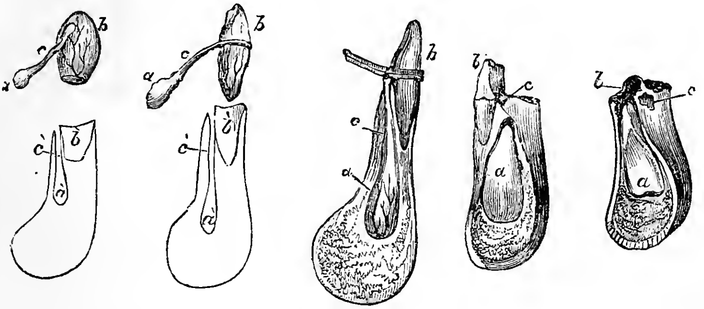


Fig. 487.—SKETCHES SHOWING THE RELATIONS OF THE TEMPORARY AND PERMANENT DENTAL SACS AND TEETH (after Blake, with some additions).

The lower parts of the first three figures, which are somewhat enlarged, represent sections of the lower jaw through the alveolus of a temporary incisor tooth: *a*, indicates the sac of the permanent tooth; *c*, its pedicle; *b*, the sac of the milk tooth or the milk tooth itself; *a'*, *b'*, indicate the bony recesses in which the permanent and temporary teeth are lodged, and *c'*, the canal by which that of the former leads to the surface of the bone behind the alveolus of the temporary tooth. The fourth and fifth figures, which are nearly of the natural size, show the same relations in a more advanced stage, in IV., previous to the change of teeth, in V., when the milk tooth has fallen out and the permanent tooth begins to rise in the jaw; *c*, the orifice of the bony canal leading to the place of the permanent tooth.

milk teeth. In the meantime, a papilla is formed at the bottom of each enamel-germ, (that for the central incisor appearing first, at about the sixth month,) and the germs become each inclosed within a dental sac, the sac of the permanent tooth adhering to the back of that for the temporary tooth. The bony socket not only forms a cell for the reception of the milk-sac, but also a small posterior recess or niche for the permanent tooth-sac, with which the recess keeps pace in its growth. In the lower jaw, to which our description may now, for convenience, be confined, the permanent sac is at length found at some distance below and behind the milk-tooth; the sac for the permanent tooth acquiring at first a pear-shape, and being then connected with the gum by a solid pedicle of fibrous tissue (fig. 487, I., II., *c*). The recess in the jaw (*a'*) has a similar form, drawn

out into a long canal for the pedicle, which opens on the edge of the jaw, by an aperture behind the corresponding milk-tooth. The permanent tooth is thus separated from the socket of the milk-tooth by a bony partition, which, as well as the root of the milk-tooth just above it, becomes absorbed as the crown of the permanent tooth rises through the gum. When this has proceeded far enough, the milk-tooth becomes loosened, falls out or is removed, and the permanent tooth takes its place. The absorption of the dental substance commences at or near the ends of the fangs, and proceeds upwards until nothing but the crown remains. The cement is first attacked, and then the dentine: but the process is similar in the two tissues. The change is not produced merely by pressure, but, as in the case of the absorption of bone, through the agency of multinucleated absorbing cells or osteoclasts, developed at the time, and applied to the surface of the fang. The sockets begin to be formed around the neck of the tooth as soon as the crown projects, and are formed simultaneously with the developing fangs.

Fig. 488.

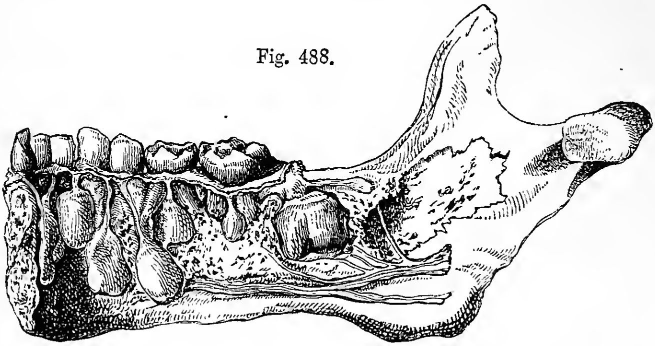


Fig. 488.—Part of the lower jaw of a child of three or four years old, showing the relations of the temporary and permanent teeth.

The specimen contains all the milk-teeth of the right side, together with the incisors of the left; the inner plate of the jaw has been removed, so as to expose the sacs of all the permanent teeth of the right side, except the eighth or wisdom tooth, which is not yet formed. The large sac near the ramus of the jaw is that of the first permanent molar, and above and behind it is the commencing rudiment of the second molar.

The six posterior (or *superadded*) permanent teeth, that is, the three permanent molars on each side, do not come in the place of other teeth. They arise from successive extensions of the enamel-germ carried backwards in the jaw behind the milk-teeth.

The part of the common enamel-germ posterior to the last temporary molar long continues unobliterated, and from it there becomes developed at about the fifteenth week of embryonic life a special enamel-germ which forms the rudiment of the first permanent molar tooth. After a long interval, viz., about the seventh month after birth, the germ for the second permanent molar tooth appears projecting backwards from the neck of that for the first molar. After another long interval, during which the sac of the first permanent molar and its contained tooth have acquired great size, and that of the second molar has also advanced considerably in development, the same changes once more occur and give rise to the sac and papilla of the wisdom-tooth (third year). The subsequent development of the permanent molar teeth takes place within their sacs just like that of the other teeth.

Calcification begins first in the anterior permanent molar teeth. Its order and periods may be thus stated for the upper jaw, the lower being a little earlier: First molar, five or six months after birth; central incisor, a little later; lateral incisor and canine, eight or nine months; two bicuspids, two years or more; second molar, five or six years; third molar, or wisdom-tooth, about twelve years.

Eruption of the permanent Teeth.—The time at which this occurs in regard to each pair of teeth in the lower jaw is exhibited in the subjoined table. The corresponding teeth of the upper jaw appear somewhat later.

Molar, first	6 years.
Incisors, central	7 ,,
,, lateral	8 ,,
Bicuspids, anterior	9 ,,
,, posterior	10 ,,
Canines	11 to 12 ,,
Molars, second	12 to 13 ,,
,, third (or wisdom)	17 to 25 ,,

It is just before the shedding of the temporary incisors—*i.e.*, about the sixth year, that there is the greatest number of teeth in the jaws. At that period there are all the milk-teeth, and the crowns of all the permanent set except the wisdom-teeth, making forty-eight (see fig. 489).

During the growth of the teeth the jaw increases in depth and length, and undergoes changes in form. In the child it is shallow, but it becomes much deeper in the adult. In the young subject the alveolar arch describes almost the segment of a circle; but in the adult the curve is semi-elliptical. The increase which takes place in the length of the jaw arises from a growth behind the posi-

Fig. 489.

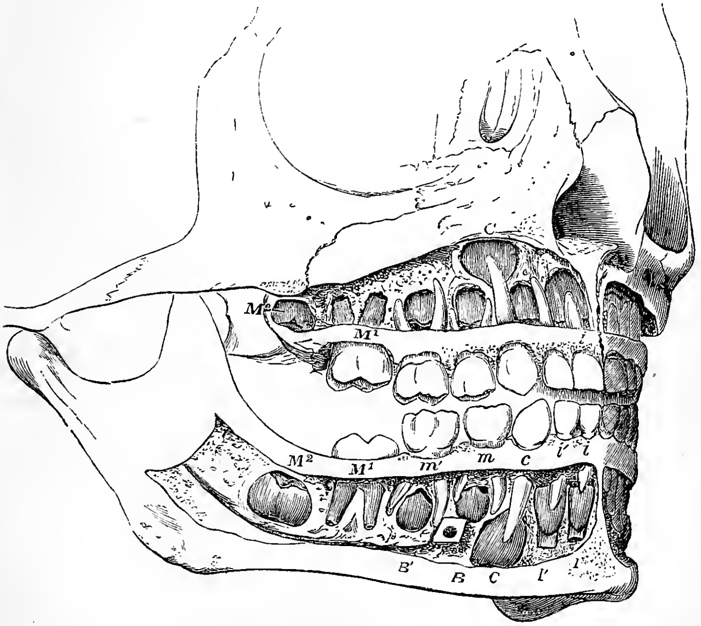


Fig. 489.—The teeth of a child of six years, with the calcified parts of the permanent teeth exposed (after Henle and modified from nature, A. T.).

The whole of the teeth of the right side are shown, together with the three front teeth of the left side: in the upper and lower jaws the teeth are indicated as follows, viz.:—1, *milk-teeth*—*i*, inner or first incisor; *i'*, outer or second incisor; *c*, canine; *m*, first molar; *m'*, second molar. 2, *permanent-teeth*—I, inner or first incisor; I', outer or second incisor; C, canine; B, first bicuspid; B', second bicuspid; M^1, the first molar, which has passed through the gums; M^2, the second molar, which has not yet risen above the gums: the third molar is not yet formed.

tion of the milk-teeth, so as to provide room for the three additional teeth on each side belonging to the permanent set. At certain periods in the growth of the jaws there is not sufficient room in the alveolar arch for the growing sacs of the permanent molars; and hence the latter are found enclosed in the base of the coronoid process of the lower jaw, and in the maxillary tuberosity of the upper jaw, but they afterwards successively assume their ultimate position as the bone increases in length. The space taken up by the ten anterior permanent teeth very nearly corresponds with that which had been occupied by the ten milk-teeth; the difference in width between the incisors of the two sets being compensated for by the smallness of the bicuspids in comparison with the milk-molars to which they succeed. Lastly, the angle formed by the ramus and body of the lower jaw differs at different ages; thus it is obtuse in the infant, approaches nearer to a right angle in the adult, and again becomes somewhat obtuse in old age (see Vol. I.).

SECONDARY DENTINE.

Under this head are included certain varieties of hard tissue liable to be formed in the pulp-cavity of a tooth after the regular production of the dentine is completed. The two chief kinds hitherto described, are the following:—

1. **Osteodentine** (Owen).—This is a hard substance which sometimes becomes deposited within the pulp-cavity, somewhat resembling bone in structure. It is traversed by canals, which contain blood-vessels and pulp-tissue, and may be surrounded by concentric lamellæ like the Haversian canals of bone. From these canals, numerous tubules radiate, larger than the canaliculi of bone, resembling, in this respect, and also in their mode of ramification, the tubes of the dentine. It may or may not coalesce with the previously formed dentine.

Fig. 490.

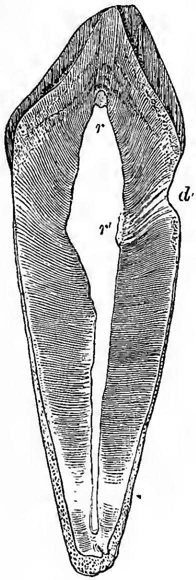


Fig. 490.—Longitudinal section of incisor tooth showing dentine of repair. Slightly magnified. (Reduced from Salter.)

d, *d'*, denuded surfaces of dentine; *r*, *r'*, corresponding deposits of secondary dentine. Two or three incremental lines are observed in the dentine.

2. **Dentine of Repair** (Salter).—When the outer surface of the dentine becomes denuded at any place, so that the peripheral ends of the tubules are there exposed, as may happen in the crown from injury or wear of the enamel, or at the cervix from continued friction and abrasion of the cement, a deposition of dentinal matter occurs on the inner surface of the dentine exactly corresponding in position and extent with the area occupied by the central ends of the exposed tubules. Many of the affected tubules become subsequently filled up by a deposit of hard matter within them, so that on section both the secondary dentine and the corresponding part of the primary dentine appear clearer and more transparent than the remainder of the dentinal substance (see fig. 490).

When the surface-injury has been considerable, the dentine of repair is largely in excess, and may in such cases completely fill up the pulp-cavity.*

* In some of the lower animals other kinds of dentine are found; for a description of these, and many other details regarding the structure and development of the teeth which could not conveniently be introduced here, the student is referred to the excellent "Manual of Dental Anatomy" by C. S. Tomes, F.R.S.

Recent Literature of the Teeth.—*Waldeyer*, in Stricker's Handbook, 1870; *Kollmann*, Ue. Linien in Schmeltz u. Cement, München Sitzungsb., 1871; Zahnbein, Schmeltz u. Cement, Zeit. f. wiss. Zool. XXIII.; *C. S. Tomes*, on the cuticula dentis, Qu. J. micr. Sci., 1872; On the dev. of the teeth, same journal, 1876; On vascular dentine, Proc. Roy. Soc., 1877, and Phil. Trans., 1878; *Magitot et Legros*, Follicule dent. chez les mammif., J. de l'anat., 1873; *Salter*, Dental Pathology, 1874; *Magitot*, Determ. de l'âge, &c., Compt. rend. LXXVIII., 1874; Struct. et dev. du tiss. dent., Compt. rend., XC., 1880; *Lambert*, in Bull. de l'acad. roy. de Belg., XLIII., 1877 (teeth of diff. races of mankind); *Epstein*, Ue. Epithel-perlen, &c., in Zeitschr. f. Heilk., I., 1880. The older literature will be found at the end of Waldeyer's article in "Stricker's Handbook," and other references in Tomes' "Dental Anatomy."

THE TONGUE.

The **tongue** is a muscular organ covered with mucous membrane. Posteriorly it is connected with the hyoid bone, and the back part of its upper surface forms the floor of the arch of the fauces; inferiorly it receives from base to apex the fibres of the genio-glossus muscle, and through the medium of that muscle is attached to the lower jaw.

Mucous membrane.—On the *under surface* of the tongue the mucous membrane is smooth and thin. It forms a fold in the middle line called the *frænum linguæ*, in front of the anterior border of the genio-glossi muscles. On each side below, as the mucous membrane passes from the tongue to the inner surface of the gums, it covers the sublingual gland. In front of the frænum, the ranine vein may be distinctly seen on each side through the mucous membrane, and close to it lies the ranine artery. Further out is an elevated line with a fimbriated margin directed outwards, which extends to the tip. The ducts of the right and left submaxillary glands end by papillary orifices close together, one on each side of the frænum; and further back, between the sides of the tongue and the lower jaw, are the orifices of the several ducts belonging to the sublingual glands.

The *upper surface* or *dorsum* of the tongue (fig. 491), is convex in its general outline, and is marked along the middle for nearly its whole length by a slight furrow called the *raphe*, which indicates its bilateral symmetry. About an inch from the base of the tongue, the raphè often terminates in a depression, closed at the bottom, which is called the *foramen cæcum* (Morgagni), and in which several small glands open. Three folds, named the glosso-epiglottic folds or frænula, of which the middle one is the largest (frænum epiglottidis), pass backwards from the base of the tongue to the epiglottis.

Papillæ.—The upper surface of the tongue in front of the foramen cæcum (the anterior two-thirds) is covered with small eminences named *papillæ*. They are found also upon the tip and borders, where, however, they gradually become smaller, and towards its under surface they disappear. The papillæ are of three kinds, *circumvallate*, *fungiform* and *conical*, varying both in size and form, but all of them visible to the naked eye; they themselves, like the rest of the mucous membrane of the tongue and mouth generally, are covered with closely set, microscopic secondary papillæ hidden under the epithelium, which correspond with those of the skin, and are each occupied by a long loop of capillary blood-vessels. Lymphatics also originate within the papillæ and pass as elsewhere in the mouth into a superficial plexus in the mucous membrane, from which again the lymph is conveyed away by valved vessels seated in the submucous tissue.

Papillæ.—The large **circumvallate papillæ** (fig. 491, 1, 2), from seven to twelve in number, are found on the back part of the tongue, arranged in two rows, which run obliquely backwards and inwards, and

Fig. 491.

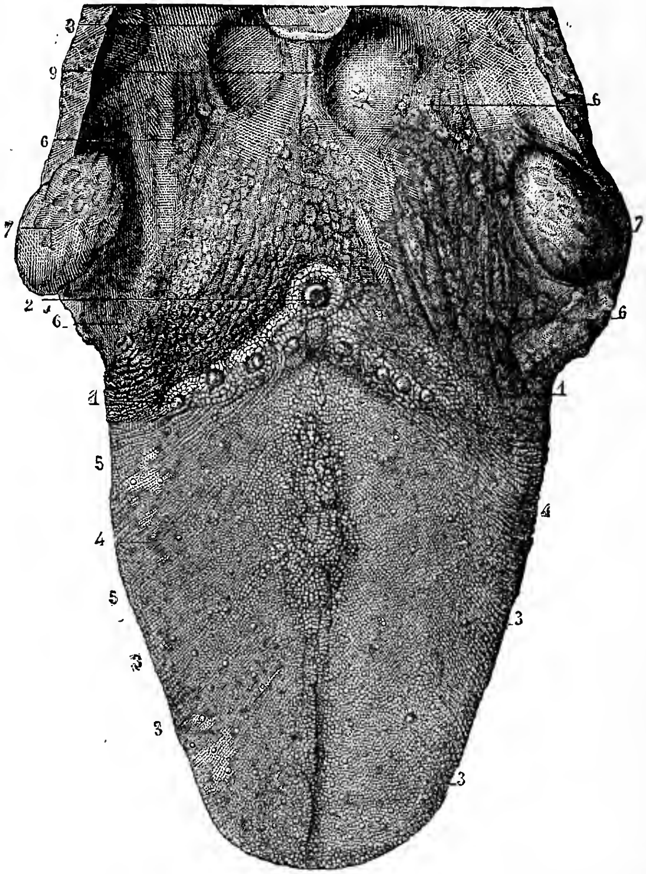


Fig. 491.—Papillary surface of the tongue, with the fauces and tonsils (from Sappey).

1, 2, circumvallate papillæ; in front of 2, the foramen cæcum; 3, fungiform papillæ; 4, filiform and conical papillæ; 5, transverse and oblique ranges; 6, mucous glands at the base of the tongue and in the fauces; 7, tonsils; 8, part of the epiglottis; 9, median glosso-epiglottic fold or frænum epiglottidis.

meet towards the foramen cæcum, like the arms of the letter V. They are situated in cup-like depressions of the mucous membrane, and have the shape of a truncated cone, of which the smaller end is attached to the bottom of the cavity, and the broad flattened base appears on the surface (fig. 492). They are therefore surrounded by a circular trench (*fossa*), around which again is an annular elevation of the mucous mem-

brane (*vallum*), and in some of them there is found a central depression, into which the ducts of one or more glands open. The stratified epithelium covering the papillæ vallatæ is thick, and completely conceals the minute secondary papillæ.

Fig. 492.

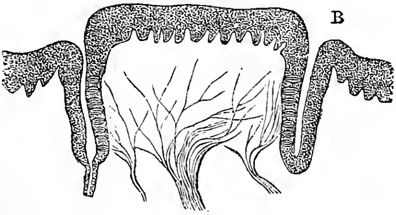


Fig. 492.—Vertical section of circumvallate papilla from the calf (Engelmann). 25 diameters.

A, the papilla ; B, the surrounding wall. The figure shows the nerves of the papilla spreading towards the surface, and towards the taste-buds which are imbedded in the epithelium at the sides ; in the sulcus on the left the duct of a gland is seen to open.

Taste-buds.—Forming a zone around the sides of the papilla, and in man and some animals upon the opposed wall of the vallum, are found, imbedded in this thick epithelium, peculiar ovoidal or flask-shaped bodies, composed of modified epithelium-cells and believed to be special organs of taste. These *taste-buds*, as they have been termed, are comparable in form and structure to the leaf-buds of a plant (fig. 493). By their bases they are in contact with the corium, while their apices, which appear as round openings or pores when viewed from the surface, emerge between the ordinary epithelium-cells. The latter are flattened around the taste-buds, enclosing them in a sort of nest. The taste-buds themselves may be described as consisting of a cortical and a central part. The cells composing the cortical part are long and flattened with tapering ends (fig. 494 *c*), and are in contact by their edges, extending from base to apex of the organ (fig. 493); they are disposed in more than one layer, and enclose the central part like the external scales of a leaf-bud. The enclosed or central cells (fig. 494 *a*) are spindle-shaped, having an enlargement near the middle where the nucleus is situated, and being prolonged at each end by a process, one of which extends upwards towards the apex of the taste-bud, and is surmounted by a fine styliform extremity which projects at the orifice, whilst the other, which is more slender and sometimes branched near its extremity, passes down into the corium of the mucous membrane, and is described as being connected with a plexus of fine nervous fibrils found in this situation. The similarity of these central *gustatory cells* to the "olfactory cells" of Max Schultze will be at once apparent.

Fig. 493.

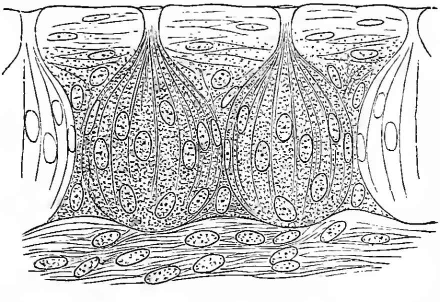


Fig. 493.—Two taste-buds from the papilla foliata of the rabbit. 450 diameters (Engelmann).

The taste-buds were discovered by Lovèn and Schwalbe, independently of each other. They have now been found on the sides (but rarely on the upper surface) of the papillæ vallatæ of a great number of animals, and are seen also on some of the fungiform papillæ to be immediately described, as well as in parts of the mucous membrane apart from papillæ both on the posterior part and sides of the tongue, and also on the soft palate, on the epiglottis, and even within the upper aperture of the larynx. According to Krause the distribution of the taste-buds follows that of the glosso-pharyngeal nerve. Their structure is most readily studied in the rabbit and hare, for in these animals there is found at each side

Fig. 494.

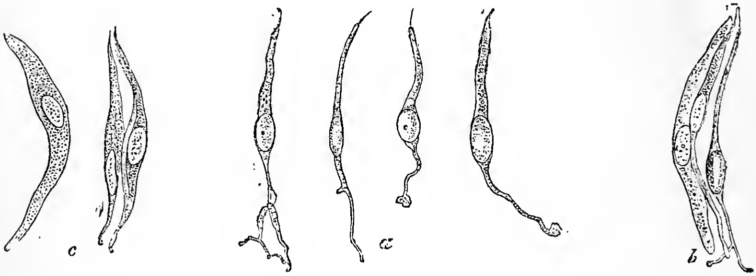


Fig. 494.—VARIOUS CELLS FROM TASTE-BUD OF RABBIT. 600 DIAMETERS (Engelmann).

a, Four cells from central part ; *b*, two cortical cells, and one central cell, in connection ; *c*, three cells from cortical part.

of the base of the tongue an oval laminated structure, the so-called *papilla foliata*, the laminæ composing which contain in the epithelium of their opposed surfaces great numbers of those bodies. A small area, situated just in front of the anterior pillar of the fauces, of variable appearance, but usually with five longitudinal folds, which are studded with taste-buds, exists in the human tongue, and is regarded as representing a papilla foliata.

According to Engelmann, each taste-bud is composed of from 15 to 30 cells.

The taste organs of the amphibia have been longer recognised. They occur in the form, not of buds but of patches interspersed here and there amongst the ordinary ciliated and columnar epithelium which covers the upper surface and sides of the tongue.

Flask-shaped bodies, resembling the taste-buds in structure, were long since described by Leydig as occurring in fishes. They are found both in the skin and in the mucous membrane of the mouth, and are believed to be gustatory organs.

The **fungiform papillæ**, more numerous than the last, are small rounded eminences scattered over the middle and fore part of the dorsum of the tongue (fig. 491, 3) ; but they are found in greater numbers and closer together at the apex and near the borders. They are easily distinguished in the living tongue owing to their deep red colour. They are narrow at their point of attachment, but are gradually enlarged towards their free extremities, which are blunt and rounded (fig. 495).

The **conical papillæ** are the most numerous of all, as well as the smallest. They are minute, conical, tapering, or cylindrical eminences, which are densely set over the greater part of the dorsum of the tongue (fig. 491, 4), but towards the base gradually disappear. They are arranged in lines diverging from the raphè, at first in an oblique direc-

tion like the two ranges of papillæ vallatæ, but gradually becoming transverse towards the tip of the tongue. At the sides they are longer and

Fig. 495.

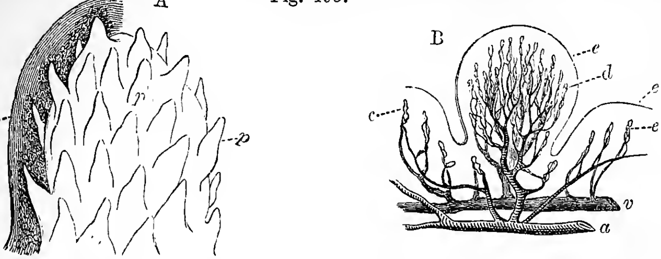


Fig. 495.—Surface and sectional view of a fungiform papilla (from Kölliker after Todd and Bowman).

A, the surface of a fungiform papilla partially denuded of its epithelium (35 diameters); *p*, secondary papillæ ; *e*, epithelium.

B, a fungiform papilla with the blood-vessels injected. *a*, artery; *v*, vein; *c*, capillary loops of simple papillæ in the neighbourhood, covered by the epithelium ; *d*, capillary loops of the secondary papillæ ; *e*, epithelium.

more slender, and arranged in parallel rows, perpendicular to the border of the tongue.

Fig. 496.

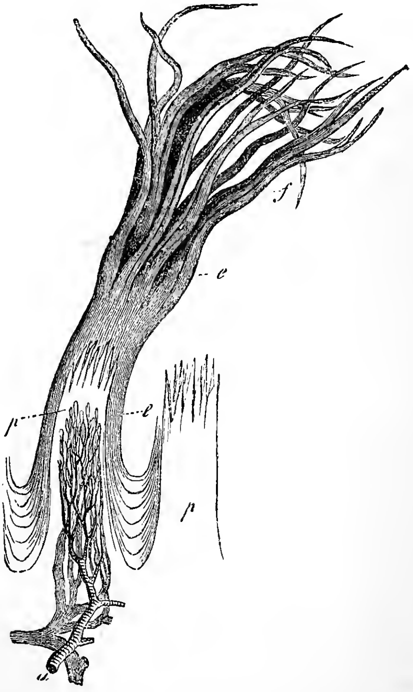


Fig. 496.—Two filiform papillæ, one with epithelium, the other without. 35 diameters. (From Kölliker, after Todd and Bowman.)

p, the substance of the papillæ divided at their upper extremities into secondary papillæ; *a*, artery, and *v*, vein, connected by capillary loops; *e*, epithelial covering, laminated between the papillæ, but extended into hair-like processes, *f*, over the secondary papillæ.

The secondary papillæ which are borne by some of the conical papillæ are peculiar both in containing a number of elastic fibres, giving them greater firmness, and in the character of their epithelial covering, which forms a separate horny process over each secondary papilla, greater in length than the papilla which it covers (fig. 496, *e*, *f*). Over some of the papillæ these processes form a pencil of fine fibres, as shown in the figure; hence the name "filiform" which has been applied to these papillæ.

The papillary surface of the tongue is supplied abundantly with nerves, some of which terminate in end-bulbs, and a few in tactile corpuscles. In the fungiform papillæ the nerves are large and numerous; but they are still more abundant, and of greater size, in the circumvallate papillæ, where they are chiefly distributed in the neighbourhood of the taste-buds (fig. 492).

The papillæ, besides being the parts chiefly concerned in the special sense of taste, also possess, in a very acute degree, tactile sensibility; and the conical and filiform papillæ, armed with their denser epithelial covering, serve a mechanical purpose, in the action of the tongue upon the food, as is well illustrated by the more developed form which these papillæ attain in many carnivorous animals.

Glands.—The mucous membrane of the tongue is provided with numerous small glands (*lingual glands*), collected principally about the posterior part of its upper surface, near the papillæ vallatæ and foramen cæcum, into which last the ducts of several open. These glands have usually been supposed to secrete mucus, but it has been ascertained that some of them, especially those which open in the trenches around the

Fig. 497.

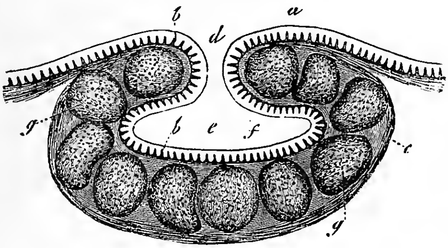


Fig. 497.—Section of a lymphoid crypt from the root of the tongue. 30 diameters. (Kölliker.)

a, epithelial lining; *b*, papillæ of the mucous membrane; *c*, outer part of the crypt, formed of connective tissue; *d*, outlet, and *e*, cavity of the crypt; *g*, surrounding follicles.

papillæ vallatæ, and at other parts where taste-buds occur, yield a more watery secretion (Ebner). Other small glands are found also beneath the mucous membrane of the borders of the tongue. There is, in particular, a group on the under surface of the tongue on each side near the apex. They are there aggregated into a small oblong mass, out of which several ducts proceed and open in a line on the mucous membrane. Some of the glands are racemose; others acino-tubular.

The mucous membrane of the tongue, at least its posterior part, is largely composed of retiform or lymphoid tissue, which is collected at numerous points into the denser nodular masses known as follicular glands, or lymphoid follicles. The blood-vessels and lymphatics of this part of the membrane are numerous and large, but the papillæ on its surface are comparatively small, and are completely concealed by the thick superjacent epithelium. Here and there the mucous membrane exhibits recesses or crypts (fig. 497), either simple or surrounded by smaller ones which open into them. The walls of these recesses are generally studded with lymphoid nodules; and they receive many of the ducts of the mucous glands.

Muscular Substance.—The substance of the tongue is chiefly composed of muscular fibres running in various directions. Many belong to muscles which enter at its base and under surface, and attach it to other parts: these are called the *extrinsic muscles* of the tongue (hyo-glossus, chondro-glossus, genio-glossus, palato-glossus, stylo-glossus), and are elsewhere described. Others which constitute the *intrinsic* or *proper*

muscles, and are placed entirely within the substance of the organ, will be here more particularly noticed. They are as follows :—

The **superficial lingual muscle** consists mainly of longitudinal fibres, placed near the upper surface of the tongue, immediately beneath the mucous membrane, and is traceable from the apex of the organ backwards to the hyoid bone (figs. 498, 499, *l s*). The individual fibres do not run the whole of this distance, but are attached at intervals to the submucous and glandular tissues. The entire layer becomes thinner towards the base of the tongue, near which it is overlapped at the sides by a thin plane of oblique or nearly transverse fibres derived from the palato-glossus and hyo-glossus muscles.

The **inferior lingual muscle** consists of a rounded muscular band, extending along the under surface of the tongue from base to apex, and lying outside the genio-glossus, between that muscle and the hyo-glossus (fig. 499, *l i*). Posteriorly, some of its fibres are lost in the substance of the tongue, and others reach the hyoid bone. In front, having first been joined, at the anterior border of the hyo-glossus muscle, by fibres from the stylo-glossus, it is prolonged beneath the border of the tongue as far as its point.

The **transverse** muscular fibres of the tongue (figs. 498, 499, *t r*) form together with the intermixed fat a considerable part of its substance. They are found in the interval between the upper and lower longitudinal muscles, and they are interwoven extensively with the other muscular fibres. Passing outwards from the median plane, where they take origin from a fibrous septum, they reach the dorsum and borders of the tongue. In proceeding outwards, they separate, and the superior fibres incline upwards, forming a series of curves with the concavity

Fig. 498.

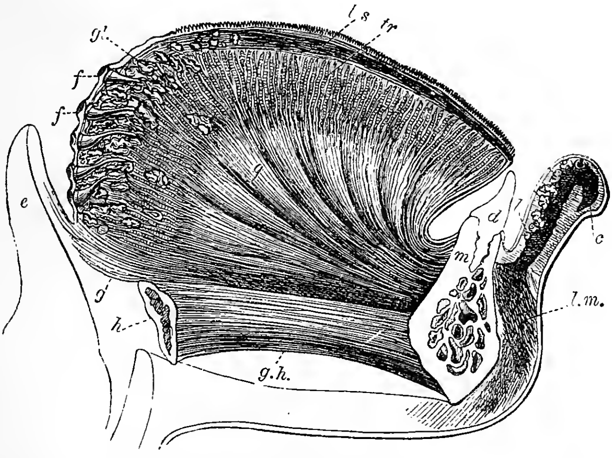


Fig. 498.—Longitudinal vertical section of the tongue, lip, &c. (from Kölliker and Arnold).

m, symphysis of the lower jaw; *d*, incisor tooth; *h*, hyoid bone; *g h*, genio-hyoid muscle; *g*, genio-hyo-glossus spreading along the whole of the tongue; *t r*, transverse muscle; *l s*, superior longitudinal muscle; *g l*, lingual glands; *f*, lymphoid crypts; *e*, epiglottis; *l*, section of the lip and labial glands; *o*, cut fibres of the orbicularis oris; *l m*, levator menti.

upwards. The fibres of the palato-glossus muscle are stated by Zaglas and Henle to be continuous with fibres of the transverse set.

Vertical fibres (external perpendicular muscle of Zaglas), decussating with the transverse fibres and the insertions of the genio-glossus (fig. 499, *h'*), form a set of curves in each half of the tongue with their concavity outwards, and extending down and out from the dorsum to the under surface of the border, so that those which are outermost are shortest.

Fig. 499.

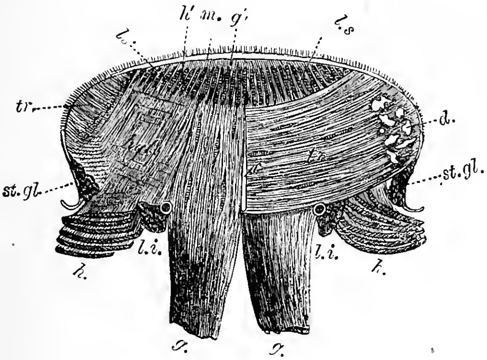


Fig. 499. — Transverse vertical section of the tongue in front of the papillæ vallatæ, seen from before (from Kölliker).

g, the genio-hyo-glossi muscles; *g'*, the vertical fibres of the right side traced upwards to the surface; *l i*, inferior longitudinal muscle with the divided ranine artery; *t r*, transverse muscle, entire on one side, but partially removed on the other, where the other muscles pass through it; *c*, septum linguæ; *h*, hyo-glossus; *h g l*, its fibres spreading upwards almost vertically outside the genio-hyo-glossus; *h'*, vertical fibres reaching the surface; *l s*, divided plates of the fibres of the superior longitudinal muscle between the vertical fibres; *s t. g l*, stylo-glossus; *d*, glands near the border of the tongue.

Examined in transverse sections, the muscular fibres are seen to be arranged so as to render the substance divisible into an outer part or *cortex* and an internal or medullary part. The fibres of the cortex are principally longitudinal, derived superiorly from the lingualis superior, further outwards from the hyo-glossus, on the side from the stylo-glossus, and beneath this from the lingualis inferior. They ensheath the medullary part on all sides except inferiorly, where the genio-glossi muscles enter it between the inferior linguales. In the medullary part are found, imbedded in fat, the decussating fibres of the transverse muscle passing across, the genio-glossi radiating upwards and outwards, and the vertical muscles arching downwards and outwards. In addition to the movements which may be given to the tongue by the extrinsic muscles, this organ is capable of being curved upwards, downwards, or laterally by its cortical fibres, it is flattened by the vertical fibres, and its margins are again drawn together by the transverse: whilst the two last mentioned, acting together, would tend to lengthen the organ.

The septum of the tongue is a thin fibrous partition which extends forwards from the hyoid bone to the tip, and divides one half of the medullary part of the tongue from the other, but does not penetrate into the cortex.

The **arteries** of the tongue are derived from the lingual, with some small branches from the facial and ascending pharyngeal. The veins empty their contents into the internal jugular trunk.

The **nerves** of the tongue (exclusive of branches from the sympathetic nerves) are three; viz., the *lingual* or *gustatory* branch of the *fifth* pair, which supplies the papillæ and mucous membrane of the fore part and sides of the tongue to the extent of about two-thirds of its surface; the lingual branch of the *glosso-pharyngeal*, which sends filaments to the mucous membrane at the base of the tongue, and especially to the papillæ vallatæ; and lastly, the *hypoglossal* nerve, which is distributed to the muscles. Microscopic ganglia exist upon the expansions of the glosso-pharyngeal nerve, especially in the neighbourhood of the

papillæ vallatæ and papillæ foliatæ, and in the sheep and calf upon the gustatory division of the fifth.

The chief lymphatic trunks accompany the ranine vessels, and after traversing one or two small lymphatic glands, seated on the hyoglossus muscle, pass into the deep cervical glands.

The detailed description of the blood-vessels and nerves will be found in the first volume.

Recent Literature (especially relating to the papillæ and taste-buds).—*Lovén*, in Arch. f. mikr. Anat., IV., 1867 ; *Schwalbe*, in the same, and in Med. Centralbl., 1868 ; *v. Wyss*, in Med. Centralbl., 1869, and in Arch. f. mikr. Anat., VI ; *Krause*, in Göttinger Nachr., 1870 ; *Hönigsschmied*, in Zeitschr. f. wiss. Zool., XXIII., 1871, and XXIX., 1877, and Med. Centralbl., 1872 ; *v. Aytai*, in Arch. f. mikr. Anat., VIII. ; *Engelmann*, Article in Stricker's Handbook ; *Ditlevsen*, Abstr. in Hofmann and Schwalbe's Jahresb., 1872 ; *v. Ebner*, "Die acinösen Drüsen der Zunge, &c.," Gratz., 1873 ; *H. Watney* (glands of tongue,) in Proc. Roy. Soc. 1874 ; *Sertoli*, in Moleschott's Unters. XI., 1874 ; *A. Hoffmann*, in Virchow's Arch., 1875 ; *Vintschgau*, Article "Geschmacksinn" in Hermann's Handbuch, 1880.

THE PALATE.

The roof of the mouth is formed by the palate, which consists of two portions ; the fore part being named the hard palate, and the back part, the soft palate.

The osseous framework of the **hard palate**, already described with the bones of the face, is covered by the periosteum, and by the lining membrane of the mouth, which are firmly connected. The mucous membrane, which is continuous with that of the gums, is thick, dense, rather pale, and much corrugated, especially in front and at the sides ; but is smoother, thinner, and of a deeper colour behind. Along the middle line is a ridge or raphè ending in front in a small eminence, which corresponds with the lower opening of the anterior palatine canal, and receives the terminal filaments of the naso-palatine and anterior palatine nerves.

The hard palate is provided with many small glands (*palatine glands*), which form a continuous layer between the mucous membrane and the periosteum ; and, like the rest of the mouth, it is covered with a squamous stratified epithelium. The corrugations of the hard palate are much better marked and more regular in the fœtus (compare Gegenbaur, Die Gaumenfalten des Menschen, Morph. Jahrb. iv., 1879).

In the rabbit fine nervous fibrils have been traced forming a plexus in the epithelium (Elin).

The **soft palate** (velum pendulum palati) is formed of a duplicature of mucous membrane inclosing muscular fibres and numerous glands. It constitutes an incomplete and moveable partition between the mouth and the pharynx, continued from the posterior border of the hard palate, obliquely downwards and backwards. Its form and its inferior connections, bounding the isthmus of the fauces, have been already described, together with the muscles which enter into its composition (Vol. I.).

The anterior or under surface of the velum, which is visible in the mouth, is concave. The mucous membrane, continuous with that of the hard palate, is thinner and redder : it is covered with a similar epithelium. The median ridge or raphè, which is continued backwards from the hard palate to the base of the uvula, indicates the original separation of the palate into two lateral halves.

The posterior surface of the soft palate, slightly convex or arched, is continuous above with the floor of the nasal fossæ. It is slightly elevated along the middle line, opposite to the uvula. The lower portion

of its mucous membrane, as well as that of the free margin of the velum, is covered with scaly, stratified epithelium; but at its upper portion the epithelium is columnar and ciliated.

In the new-born child the whole posterior surface is covered with ciliated epithelium (Klein), but this becomes subsequently replaced by squamous; the epithelium of the gland-ducts, however, retains in many instances its ciliated character.

On both surfaces of the velum are found numerous small compound glands. They particularly abound on the upper surface, where they form almost a complete layer under the mucous membrane; they are also very abundant in the uvula.

THE TONSILS.

The **tonsils** (tonsillæ, amygdalæ) are two prominent bodies, which occupy the recesses formed, one on each side of the fauces, between the anterior and posterior palatine arches (fig. 509, 23).

They are usually about half an inch in length, and a third in width and thickness; but they vary much in size in different individuals.

The free inner surface of the tonsil, projecting into the fauces between the palatine arches, has from twelve to fifteen orifices, which give it a perforated appearance. These orifices lead into recesses or crypts in the substance of the tonsil, like those already described as occurring at the back part of the upper surface of the tongue (fig. 497). The tonsils contain a large number of lymphoid follicles ranged around the walls of these crypts, and between these is a quantity of less dense lymphoid tissue. The outer side of the tonsil is connected with the inner surface of the superior constrictor of the pharynx, and approaches very near to the internal carotid artery. Considered in relation to the surface of the neck, the tonsil corresponds to the angle of the lower jaw, where it may be felt beneath the skin when it is enlarged.

These structures receive a very large supply of blood from various arteries, viz., from the tonsillar and palatine branches of the facial artery, and from the descending palatine, the ascending pharyngeal and the dorsal artery of the tongue. From these arteries fine branches and capillaries are distributed abundantly to the lymphoid tissue and follicles and to the papillæ of the mucous membrane which lines the recesses. The veins are numerous, and enter the tonsillar plexus on its outer side. The nerves come from the glosso-pharyngeal nerve, and from the fifth pair. Lymphatics are abundant, and surround the follicles with a close plexus; they eventually pass into the superior deep cervical lymphatic glands.

THE SALIVARY GLANDS.

The saliva, which is poured into the mouth, and there mixed with the food during mastication, is secreted by three pairs of glands, named from their respective situations, *parotid*, *submaxillary*, and *sublingual*. Agreeing in their general physical characters and minute structure, these glands differ in their size, form, and position.

The Parotid Gland.—The parotid (fig. 500, *p*) is the largest of the three salivary glands. It lies on the side of the face, in front of the ear, and extends deeply into the space behind the ramus of the lower jaw. Its weight varies from five to eight drachms.

Its outer surface is convex and lobulated, and is covered by the skin and fascia, and partially by the platysma muscle. It is bounded above by the zygoma, below by a line drawn backwards from the lower border of the jaw to the sterno-mastoid muscle, and behind by the external meatus of the ear, the mastoid process, and sterno-mastoid muscle. Its

anterior border, which lies over the ramus of the lower jaw, is less distinctly defined, and stretches forwards to a variable extent on the masseter muscle. It is from this anterior border of the gland that the excretory duct passes off; and there is frequently found in connection with the duct, and lying upon the masseter muscle, a small process or a separated portion of the gland (p'), which is called *glandula socia parotidis*. On trying to raise the deeper part of the parotid gland from its position, it is found to extend far inwards, between the mastoid process and the ramus of the jaw, towards the base of the skull, and to be intimately connected with several deep-seated parts. Thus, above, it reaches into and

Fig. 500.

Fig. 500.—Sketch of a superficial dissection of the face, showing the position of the parotid and submaxillary glands (Allen Thomson). $\frac{2}{5}$

p, parotid gland ; *p'*, socia parotidis ; *d*, the duct of Stenson before it perforates the buccinator muscle ; *a*, transverse facial artery ; *n*, *n*, branches of the facial nerve emerging from below the gland ; *f*, the facial artery passing out of a groove in the sub-maxillary gland and ascending on the face ; *s m*, superficial portion of the submaxillary gland.

occupies the posterior part of the glenoid cavity; behind and below, it touches the digastric muscle, and rests on the styloid process and styloid muscles; and, in front, under cover of the ramus of the jaw, it advances a certain distance between the external and internal pterygoid muscles.

The internal carotid artery and internal jugular vein are close to the deep surface of the gland. The external carotid artery, accompanied by the temporo-maxillary vein, passes through the parotid gland, and in that situation divides into the temporal and internal maxillary arteries, the former soon giving off its auricular and transverse facial branches.

The gland is also traversed by the facial nerve, which divides into branches within its substance, and it is pierced by branches of the great auricular nerve.

The **parotid duct**, named also **Stenson's duct** (d. Stenonianus), appears at the anterior border of the gland, about one finger's breadth below the zygoma, and runs forwards over the masseter muscle, accompanied by the socia parotidis, when that accessory portion of the gland exists, and receiving its ducts. At the anterior border of the masseter, the duct (*d*) turns inwards through the fat of the cheek and pierces the buccinator muscle; and then, after running for a short distance obliquely forwards beneath the mucous membrane, opens upon the inner surface of the cheek, by a small orifice on a papilla opposite the crown of the second molar tooth of the upper jaw. Its direction across the face may be indicated by a line drawn from the lower margin of the concha of the ear to a point midway between the red margin of the lip and the ala of the nose. The length of the Stenonian duct is about two inches and a half, and its diameter rather less than $\frac{1}{8}$th of an inch. At the place where it perforates the buccinator, its canal is as large as a crow-quill, but at its orifice it is smaller than in any other part, and will only admit a fine probe.

The vessels of the parotid gland enter and leave it at numerous points. The arteries are derived directly from the external carotid, and from those of its branches which pass through or near the gland. The veins correspond. The lymphatics join the deep and superficial set in the neck; and there are often one or more lymphatic glands embedded in the substance of the parotid. The nerves come from the sympathetic plexus on the external carotid artery, and also from the facial, the auriculo-temporal and great auricular nerves. In the dog and cat it has been experimentally shown that the parotid derives its cerebro-spinal nerve-supply from the glosso-pharyngeal, through the lesser superficial petrosal nerve and the otic ganglion, the fibres finally passing to the gland by a branch of the auriculo-temporal.

An instance is recorded by Gruber of a remarkable displacement of the parotid on one side; the whole gland being situated on the masseter muscle as if it were an enlarged socia parotidis (Virchow's Archiv, xxxii.).

The submaxillary gland.—The submaxillary gland (figs. 500, 501, *sm*), the next in size to the parotid, is of a spheroidal form, and weighs about 2 or $2\frac{1}{2}$ drachms. It is situated immediately below the base and the inner surface of the inferior maxilla, and above the digastric muscle. In this position it is covered by the skin, fascia and platysma myoides, and its inner surface rests on the mylo-hyoid, hyo-glossus, and stylo-glossus muscles; above, it corresponds with a depression on the inner surface of the jaw-bone; and it is separated behind from the parotid gland merely by the stylo-maxillary ligament. The facial artery, before it mounts over the jaw-bone, lies in a deep groove upon the back part and upper border of the gland.

The duct of the submaxillary gland, named **Wharton's duct** (*d'*, fig. 501), which is about two inches in length, leaves the main gland posteriorly, together with a thin process of the glandular substance, and passing round the posterior border of the mylohyoid muscle (*mh*), runs forwards and inwards above that muscle, between it and the hyo-glossus and genio-hyo-glossus, and beneath the sublingual gland, to reach the side of the frænum linguæ. Here it terminates, close to the duct of the opposite side, by a narrow orifice, which opens

at the summit of a soft papilla (*d*) seen beneath the tongue. The obvious structure of this gland is like that of the parotid; but its lobes are larger, its surrounding areolar web is finer, and its attachments are not so firm. Moreover, its duct has much thinner coats than the parotid duct.

The blood-vessels of the submaxillary gland are branches of the facial and lingual arteries and veins. The nerves include those derived from the submaxillary ganglion, and through this from the chorda tympani, from the lingual branch of the inferior maxillary (and in rare cases from the mylo-hyoid branch of the inferior dental nerve), and from the sympathetic.

The sublingual gland.—The sublingual gland (fig. 501), the smallest of the salivary glands, is of a narrow oblong shape and weighs scarcely one drachm. It is situated along the floor of the mouth, where it forms a ridge between the tongue and the gums of the lower jaw, covered only by the mucous membrane. It reaches from the frænum

Fig. 501.

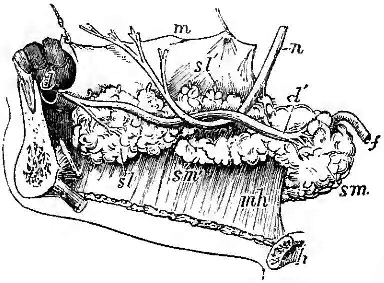


Fig. 501.—View of the Right Submaxillary and Sublingual Glands from the inside (Allen Thomson).

Part of the right side of the jaw, divided from the left at the symphysis, remains; the tongue and its muscles have been removed; and the mucous membrane of the right side has been dissected off and hooked upwards so as to expose the sublingual glands; *s m*, the larger superficial part of the submaxillary gland; *f*, the facial artery passing through it; *s m′*, deep portion prolonged on the inner side of the mylo-hyoid muscle *m h; s l*, is placed below the anterior large part of the sublingual gland, with the duct of Bartholin partly shown; *s l′*, placed above the hinder small end of the gland, indicates one or two of the ducts perforating the mucous membrane; *d*, the papilla, at which the duct of Wharton opens in front behind the incisor teeth; *d′*, the commencement of the duct; *h*, the hyoid bone; *n*, the gustatory nerve; close to it is the submaxillary ganglion.

linguæ, in front, where it is in contact with the gland of the opposite side, obliquely backwards and outwards for rather more than an inch and a half. On its inner side it rests on the genio-hyo-glossus; below, it is supported by the mylo-hyoid muscle (*mh*), which is interposed between it and the main part of the submaxillary gland; and it is here in close contact with the Whartonian duct, with the accompanying deep portion of the last-named gland, and also with the lingual branch of the fifth nerve.

The lobules of the sublingual gland are not so closely united together as those of the other salivary glands, and the ducts from many of them open separately into the mouth, along the ridge which indicates the position of the gland. These ducts, named **ducts of Rivini,** are from eight to twenty in number. Some of them open into the duct of Wharton. One, longer than the rest (which is occasionally derived in part also from the submaxillary gland), runs along the Whartonian duct, and opens either with it or very near it; this has been named the *duct of Bartholin.*

The blood-vessels of this gland are supplied by the sublingual and submental arteries and veins. The nerves are numerous, and are derived from the lingual branch of the fifth.

STRUCTURE OF THE SALIVARY GLANDS.

These glands are constructed on the compound racemose type. Their ducts (traced backwards), after branching a certain number of times, terminate in fine ramuscules, into which the alveoli open. The *alveoli* of the salivary glands do not always present the form usually regarded as typical of the alveoli of a compound racemose gland. They are sometimes dilatations of the extremities of the duct beset with saccular enlargements, sometimes more tubular and even somewhat convoluted

Fig. 502.

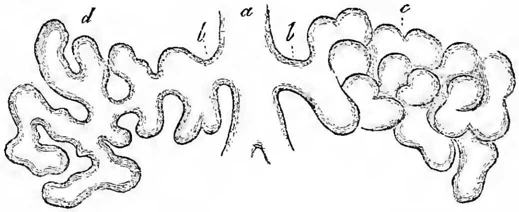


Fig. 502.—Diagram of the construction of a lobule of a tubulo-racemose (acino-tubular) mucous gland (from Kölliker).

a, duct; *b*, a branch of the duct; *c*, alveoli as they lie together in the gland; *d*, the same separated, showing their connection as an irregular tube.

without marked sacculation (fig. 502) (acino-tubular variety), but there is no essential difference between the two forms, transitions being met with between them. The alveoli are enclosed by a basement membrane, which is not complete as in many glands, but forms a basket-like investment to the alveolus, the flattened cells which form it, being ramified and united together by their branches (fig. 503). There is however in addition a delicate homogeneous substance occupying the meshes between the cells (see the left-hand alveolus in fig. 503). The cells of the basement membrane are said to send inwards processes to form a sustentacular network amongst the alveolar cells.

Fig. 503.

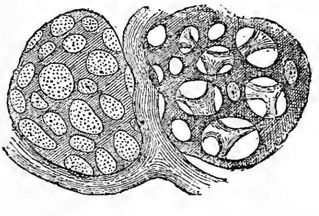


Fig. 503.—Membrana propria of two alveoli isolated (Heidenhain after Lavdovsky).

The preparation is taken from the orbital gland of the dog, which is similar in structure to a mucous salivary gland.

The alveoli are united by the blood-vessels and a small amount of loose connective tissue into lobules, and these again by a larger quantity of the same tissue into larger lobules. A considerable amount of connective tissue also accompanies the blood-vessels and duct in their ramifications through the gland. The connective tissue, where it is in larger amount, is lamellar in character (Klein), and it contains, besides the ordinary

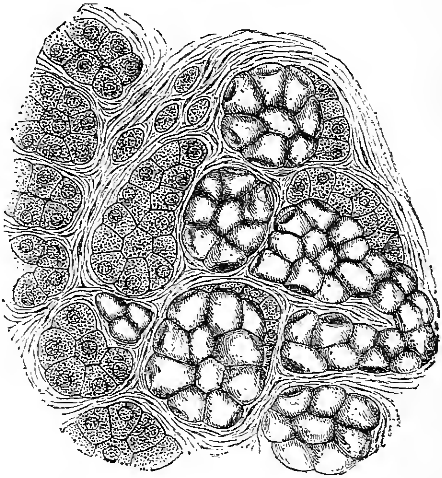
flattened cells, a certain number of granular plasma-cells and lymph-corpuscles, with fat cells occasionally.

The alveoli of the salivary glands may be divided into two classes, according to the nature of their secretion :—those of the one kind yielding a ropy secretion characterised by containing mucin, and those of the other kind, a thinner more watery secretion, sometimes containing a considerable amount of serum-albumin, so that the secretion coagulates on being heated. The two kinds of alveoli may accordingly be distinguished as *mucous* and *serous* or *albuminous*, (Heidenhain); they differ from one another both in appearance and in the nature of their secreting cells. In some cases an alveolus may contain mucous and serous cells side by side.

Fig. 504.—Section of part of the human submaxillary gland (Heidenhain).

To the right of the figure is a group of mucous alveoli, to the left a group of serous alveoli.

Fig. 504.



The human parotid and that of all mammals is composed of serous alveoli, and the sublingual gland of mucous alveoli, but in man the submaxillary is a mixed gland, containing both kinds of alveoli, although the serous are the more numerous (fig. 504). In the dog and most other animals it is purely a mucous gland, and in the rabbit and guinea pig it is purely a serous gland. Similar differences have already been noticed (p. 570) in the small glands of the tongue. In the guinea pig there are small flat mucous glands of tubular structure connected both to the parotid and submaxillary, one to each, and sending their ducts to open into the ducts of those glands (Klein).

Mucous alveoli.—In the mucous glands and mucous alveoli of mixed glands most of the alveolar cells, when the gland is in the inactive condition, appear large, clear, and almost spheroidal in shape, and nearly fill the alveoli, which are distended by the cells (right-hand side of fig. 504). The nucleus of each cell is in the part of the cell next to the basement membrane, against which it is generally flattened, and the cells may cause the basement membrane to be bulged out opposite to them. In preparations hardened in alcohol, the cells are finely granular, and with the exception of the part around the nucleus are scarcely stained by carmine (fig. 505, A).

When isolated, they not unfrequently exhibit processes, one from the base of each cell : the projection is flattened and overlaps the base of a neighbouring cell (Kölliker). The peculiar clear appearance of these cells is due to the accumulation within them of mucin (or of a substance "mucigen" from which mucin is formed) ; this substance is precipitated by acids, but swollen up, and the cells are destroyed, by the action of water or alkalies.

Besides the "mucin cells" there are met with in most alveoli of these glands, cells of a different character, which from their position may be named "marginal cells." In some mucous glands, *e.g.*, the submaxillary of the cat, they form an almost complete outer layer, next to the basement membrane, and enclosing the mucin-cells, but in the dog's submaxillary gland they occur only in small semilunar masses (lunulæ of Gianuzzi) flattened up between the basement membrane and the mucin-cells (fig. 505, A; fig. 507, *s*). These marginal-cells are small and granular, and stain deeply with carmine.

Fig. 505.

A B

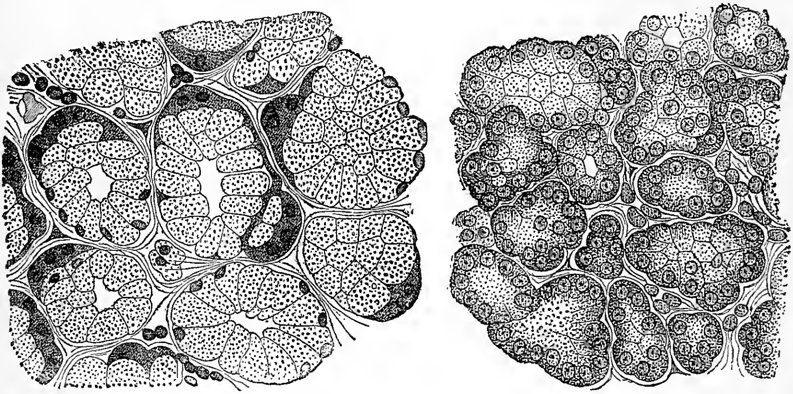


Fig. 505.—Sections of the orbital gland of the dog. A, during rest. B, after a period of activity (Heidenhain after Lavdovsky).

In A, the cells of the alveoli are large and clear, being filled with the material for secretion (in this case, mucigen) which obscures their protoplasm, but some of the cells have not participated in the formation of the secretion, and these remain small and protoplasmic, forming the crescentic group seen in most of the alveoli.

In B, the accumulated material is discharged from the cells, which appear partially disintegrated in consequence. Both the cells and the alveoli are much smaller, and the protoplasm of all the cells is now apparent.

If the mucous glands are stimulated to secretion, the mucin-cells become gradually smaller and less clear, their contents being exuded in the form of mucus, which first fills the cavity of the alveolus and then passes on into the duct. At the same time the cells are easily stained with carmine and their nuclei are no longer flattened, but assume a more rounded form and central position (fig. 505, B). If the gland be strongly urged to activity as by prolonged stimulation of its cerebral nerves, the mucin-cells may undergo still more profound alterations, and may even become partially or wholly disintegrated, and removed from the alveolus with the secretion. It is uncertain whether the whole cell may thus be destroyed, or whether the part surrounding the nucleus may not remain and regenerate the cell; this is certainly the case in some of the small mucous glands of the mouth in which no marginal cells can be seen. It is probable however that in the salivary glands, some at least of the mucin-cells are entirely destroyed, and the marginal cells multiplying and becoming filled with secretion, serve to replace those which are thus lost. In this way we may suppose that, even while the discharge of secretion is still proceeding, new secreting cells are forming, at the same time that some of the older ones are being destroyed (Heidenhain).

Serous alveoli.—In the serous glands and serous alveoli of mixed

glands, the cells, in the inactive condition of the glands, are in the fresh condition and in osmic preparations seen to be packed full of distinct granules, of an albuminous nature, which obscure their nuclei. The granules are imbedded in the protoplasm of the cells and the latter almost completely fill the alveoli, scarcely any lumen being discernible (fig. 506, A).

Fig. 506.

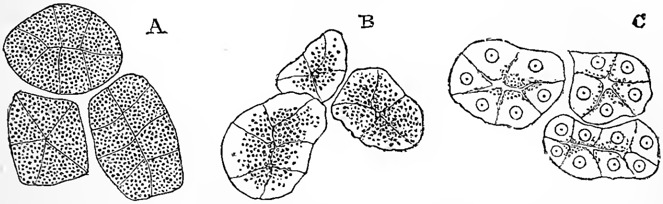


Fig. 506.—Alveoli of serous glands. A, at rest. B, after a short period of activity. C, after a prolonged period of activity. (Langley.)

After a short period of activity the granules are found to have disappeared in the outer part of the cell, the inner part being still distinctly granular and some granules being apparently free within the lumen of the alveolus, now becoming distinct (fig. 506, B). With more prolonged activity (fig. 506, C) the clear outer part increases in extent, and the granules are found only in the part of the cell which is close to the lumen, and in those parts which are contiguous to the adjacent cells, (corresponding perhaps to fine capillary clefts which pass from the cavity of the alveolus between the cells). The nuclei have now become distinct,

Fig. 507.

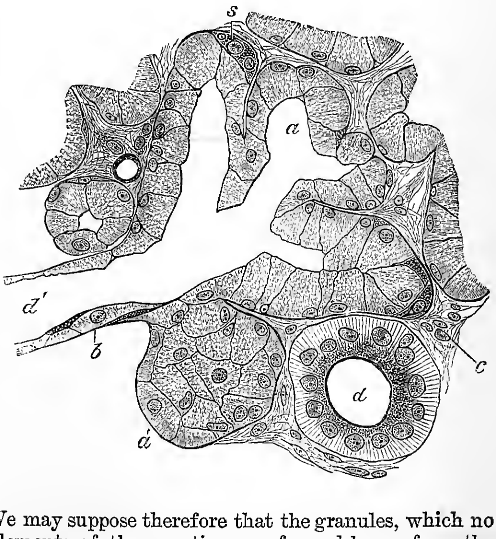


Fig. 507.—Section of the submaxillary gland of the dog, showing the commencement of a duct in the alveoli. Magnified 425 diameters. (E. A. S.).

a, one of the alveoli, several of which are in the section shown grouped around the commencement of the duct, *d'*; *a'*, an alveolus, not opened by the section; *b*, basement membrane in section; *c*, interstitial connective tissue of the gland; *d*, section of a duct which has passed away from the alveoli, and is now lined with characteristically-striated columnar cells; *s*, semilunar group of darkly-stained cells at the periphery of an alveolus.

and the cells are smaller. We may suppose therefore that the granules, which no doubt contain the specific elements of the secretion, are formed by or from the protoplasm of the cells during rest, and are discharged into the lumen and dissolved during activity. Probably however even during activity new granules are constantly being formed and passed onwards towards the lumen. According to Langley, the three processes of growth of the clear protoplasm, conversion of

this into granules, and discharge of these into the lumen, are all proceeding simultaneously in different parts of the cell during activity.

In glands which have been hardened in alcohol the granules are found to be dissolved and their place occupied by a clear substance which does not stain with carmine.

Ducts.—In the serous glands, and serous parts of mixed glands, the first or *intercalary part of the duct* which conveys the secretion from the alveoli is narrow, and lined with clear flattened cells with elongated nuclei. After a longer or shorter course, this part passes by a somewhat narrower "neck," lined with cubical cells with small nuclei, into the intralobular ducts (Klein).

In the mucous glands the intercalary ducts are also lined (fig. 507, *d'*) with clear cells continuous with the cells of the alveoli, but flattened against the basement membrane so as to leave a considerable lumen.

This first part of the duct is generally shorter than the corresponding part in the serous glands, and is regarded by Klein as representing only the part by him termed the "neck;" more probably, however, it must be looked upon as representing both parts, although they are not here so clearly differentiated. The intercalary part of the ducts is described by Klein as being lined, within the epithelium, by a special delicate nucleated membrane, which in some animals is continued into the intralobular ducts.

In the next or *intralobular part of the duct* (fig. 507, *d*) the character of the epithelium changes abruptly, the cells becoming large and columnar or conical, the rounded or truncated apex being directed towards the lumen of the tube. Each cell contains a spherical nucleus near the centre (fig. 508, *n*). The part of the cell next the lumen of the duct

Fig. 508.

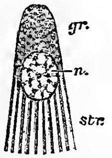


Fig. 508.—STRIATED EPITHELIUM CELL, FROM THE DUCT OF A SALIVARY GLAND; HIGHLY MAGNIFIED. SEMIDIAGRAMMATIC. (E.A.S.)

gr, granular protoplasm; *str*, striæ; *n*, nucleus.

is granular in character, whereas the part nearest the basement membrane is finely striated longitudinally. This striated appearance is most distinct in the ducts of the submaxillary gland; it is due to the presence of a rod-like or fibrillar structure in that part of the cell.

The larger ducts acquire a coating of fibrous and elastic tissue outside the basement membrane, and, except in those of the sublingual gland, a few plain muscular fibre-cells are also to be found. The columnar epithelium is here double, a second row consisting of somewhat smaller cells lying outside, and fitting between, the elongated cells which are continuous with those of the smaller ducts.

Vessels and nerves.—The blood-vessels of the salivary glands are numerous, and form a close capillary network outside the basement membrane both of the alveoli and the ducts.

The lymphatics commence in the form of lacunar clefts between and around the alveoli, lying closer to these than do the networks of blood-capillaries (Gianuzzi). The issuing lymphatics accompany the blood-vessels and ducts.

The nerves are large and numerous, and many of them exhibit minute ganglia, especially those in the dog's submaxillary. There are fewer in the human submaxillary gland, and no ganglia in the parotid (Klein). Some of them have been

observed to terminate in Pacinian corpuscles of a simple kind (Krause), and many no doubt supply the blood-vessels. There are good reasons for believing that the nerve-fibres come into intimate relation with the secreting cells of the glands, but in what manner such connection may occur is not known. According to Pflüger, the basement membrane of the alveoli, as well as of the ducts, is perforated by the nerves, which lose their medullary sheath, and, breaking up into a number of branches, become connected with the cells. Other observers, however, have failed to corroborate these statements.

The **Recent Literature** of the salivary glands is comprised in the list of works given under the article "Secreting Glands." To these may be added a recent paper by Klein, in the "Quarterly Journal for Microscopical Science," April, 1882.

THE PHARYNX.

The **pharynx** (fig. 509) extends from the base of the skull to the lower border of the cricoid cartilage, and forms a sac continued at the lower end into the gullet, with apertures in front, which lead into the nose, mouth and larynx. The velum projects backwards into it, and during the passage of the food is drawn backwards by muscular action so as completely to separate an upper from a lower part. In all, seven openings lead into the cavity of the pharynx; viz., above the velum, the two posterior openings of the nares (*choanæ narium*), and at the sides the apertures of the Eustachian tubes (fig. 509, 10); while below the velum, there is first the passage leading from the mouth; then the superior opening of the larynx, and lastly the passage into the œsophagus.

The pharynx is about 4½ inches in length, and is considerably wider across than from before backwards. Its widest part is opposite the cornua of the hyoid bone; below this it rapidly contracts like a funnel towards its termination in the gullet, opposite the cricoid cartilage, where it is narrowest.

The posterior wall of the pharynx at its upper end forms a cul-de-sac on each side opposite the tip of the petrous bone, and lies in a curve, with its convexity forwards, in front of the recti capitis antici muscles.

Attachments.—The walls of the pharynx are formed by a fascia or layer of fibrous tissue, named the pharyngeal aponeurosis, dense at its upper part but lax and weak below, which is covered by muscles and lined by mucous membrane. At its upper end this fibrous wall is attached to the posterior part of the body of the sphenoid bone, and passes outwards to the petrous portion of the temporal bone and on to the Eustachian tube. It is strengthened in the middle line by a strong band descending between the recti antici muscles from a part of the basilar process of the occipital bone, which often presents a marked tubercle (*pharyngeal tubercle*, see vol. i.).

Behind, the pharynx is loosely connected by areolar tissue to the pre-vertebral fascia covering the bodies of the cervical vertebræ and the muscles which rest upon them. At the sides it has similar connections with the styloid process and its muscles, and with the sheaths of the large vessels and nerves of the neck. In front, it is attached in succession to the sides of the posterior nares, the mouth and the larynx.

Thus commencing above by a tendinous structure only, the pharynx is connected by means of muscle and fibrous membrane, first, with the internal pterygoid plate

then with the pterygo-maxillary ligament, and next with the mylo-hyoid ridge of the lower jaw; below this, it is attached to the sides of the tongue, to the hyoid bone, and stylo-hyoid ligament; and, still lower down, to the thyroid and cricoid cartilages.

Structure.—The *muscles* of the pharynx are the superior, middle and inferior constrictors, the stylo-pharyngeus, and the palato-pharyngeus. They have already been described in vol. i.

Fig. 509.

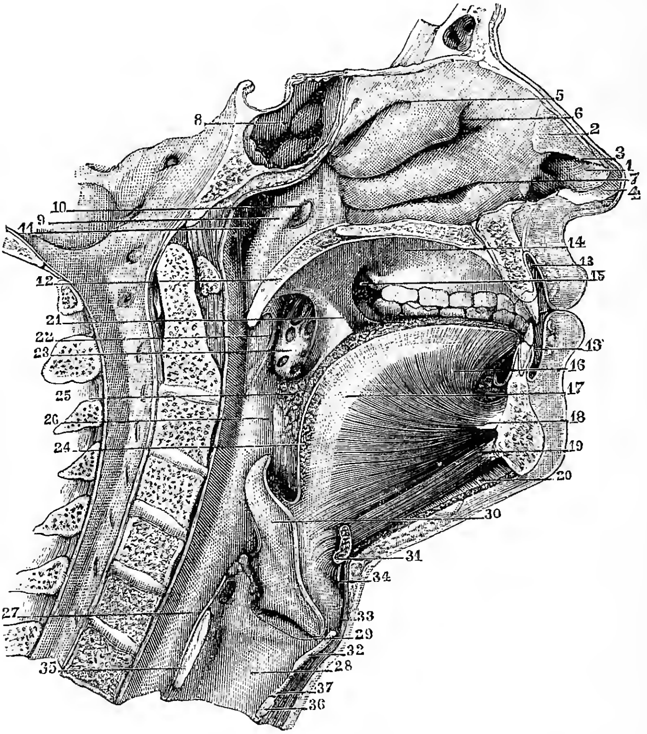


Fig. 509.—Median section of the mouth and pharynx (Sappey).

1 to 8, relate to parts in connection with the nostrils; 9, upper or respiratory part of the pharynx; 10, aperture of the left Eustachian tube; 11, depression of the mucous membrane; 12, velum palati; 13, 13, vestibulum oris; 14, arch of the palate; 15, space at the back of the dental series; 16, 17, tongue; 18, genio-glossus; 19, genio-hyoid; 20, mylo-hyoid, cut; 21, 22, anterior and posterior pillars of the fauces; 23, tonsil; 24, posterior vertical part of the tongue; 25, its glandular eminences and depressions; 26, 27, lower part of the pharynx; 28 to 37, refer to parts of the larynx; 30, epiglottis.

The *mucous membrane* is continuous at the several apertures with that of the adjacent cavities. It varies somewhat in its character in different parts. Its upper portion, which presents numerous folds with intervening recesses, is thick where it adheres to the base of the skull, but much

thinner near the entrance of the Eustachian tubes and the posterior nares: in this situation numerous racemose mucous glands are found collected in a layer beneath the mucous membrane. Lymphoid follicles also exist throughout the whole of the pharynx.

A collection of these, forming a glandular mass similar to that composing the tonsils, stretches across the back of the pharyngeal cavity between the orifices of the two Eustachian tubes (Kölliker).

A well-marked recess of the mucous membrane, known as the *bursa pharyngea*, which is constant in the fœtus and young subject, is occasionally present in the adult in the middle line posteriorly, extending as far upwards as the pharyngeal tubercle. It opens by a narrowed orifice below the glandular mass just mentioned. (Compare *v. Teutleben*, Die Tubentonsille, in Zeitschr. f. Anat. u. Entw., 1876; and *Ganghofner*, Ue. d. Tonsilla u. Bursa pharyngea, in Wiener Sitzungsb. LXXVIII. 1878). (For the description of a remarkable case of lateral diverticulum of the pharynx, see a paper by M. Watson in the Journal of Anat. and Physiol., 1874.)

In the part opposite the fauces, the mucous membrane exactly resembles that of the mouth. Lower down it becomes paler, and at the back of the larynx it forms several longitudinal folds. The epithelium upon the upper portion of the pharynx, nearly as low down as the base of the uvula, is columnar and ciliated; but, below that point, it is scaly and stratified. In the fœtus the ciliated epithelium has a more extensive distribution, and it often persists in the recesses and gland ducts of all parts of the pharynx.

THE ŒSOPHAGUS.

The **œsophagus** or **gullet,** the passage leading from the pharynx to the stomach, commences at the cricoid cartilage opposite the sixth cervical vertebra, and passing through the diaphragm opposite the tenth or eleventh dorsal vertebræ, there ends by opening into the stomach.

The length of the œsophagus is about 9 or 10 inches. It is of smaller diameter than any other division of the alimentary canal, its narrowest part being at the commencement behind the cricoid cartilage; it is also slightly constricted in passing through the diaphragm, but, below that, widens into the stomach. It is not quite straight in its direction, but has three slight curvatures. One of these is an antero-posterior flexure, corresponding with that of the vertebral column in the neck and thorax. The other two are slight lateral curves; for the œsophagus, commencing in the median line, inclines to the left side as it descends to the root of the neck; thence to the fifth dorsal vertebra it gradually resumes the mesial position; and finally, it deviates again to the left, at the same time coming forward towards the œsophageal opening of the diaphragm.

Connections.—In the lower cervical and upper dorsal region the œsophagus is applied to the anterior surface of the spine, being connected with it and with the longus colli muscle by loose areolar tissue; between it and the bodies of the dorsal vertebræ the thoracic duct ascends obliquely from right to left; in its lower third it is placed in front of the aorta. In the neck, the œsophagus lies close behind the trachea, (projecting about a quarter of an inch to the left of that tube), and the recurrent laryngeal nerve ascends on either side in the angle between them; on each side is the common carotid artery, and also a part of the thyroid body, but, as the œsophagus inclines to the left side, it is in more immediate connection with the left carotid. In the thorax, the œsophagus is successively

covered in front by the lower part of the trachea, by the commencement of the left bronchus, and by the pericardium. The aorta, except near the diaphragm, where the œsophagus is in front of the vessel, lies to the left, and the vena azygos to the right and behind; the pneumogastric nerves descend in close contact with its sides, and form a plexus around it, the left nerve proceeding gradually to the front, and the right nerve retiring behind it. Lastly, the œsophagus, which is here placed in the interval between the two pleuræ, comes partially in contact with both of those membranes but more extensively on the right side.

STRUCTURE OF THE ŒSOPHAGUS.

The walls of the gullet are composed of three coats; viz., an external or muscular, a middle or areolar, and an internal or mucous coat. Outside the muscular coat there is a layer of areolar tissue, with well marked elastic fibres.

The **muscular coat** consists of an *external longitudinal layer* (seen in section in fig. 510, *b*) and an *internal* circular layer (*c*). This twofold arrangement of the muscular fibres prevails throughout the whole length of the alimentary canal; but the two layers are here much thicker, more uniformly disposed, and more evident than in any other part, except quite at the lower end of the intestine. The external or *longitudinal* fibres are disposed at the commencement of the tube in three bands,

Fig. 510.

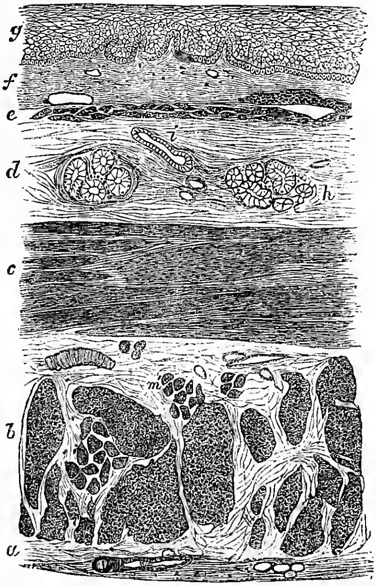


Fig. 510.—Section of the human œsophagus. (V. Horsley).

The section is transverse, and from near the middle of the gullet. *a*, fibrous covering; *b*, divided fibres of the longitudinal muscular coat; *c*, transverse muscular fibres; *d*, submucous or areolar layer; *e*, muscularis mucosæ; *f*, mucous membrane, with vessels and part of a lymphoid nodule; *g*, laminated epithelial lining; *h*, mucous gland; *i*, gland duct; *m'*, striated muscular fibres cut across.

one in front, and one on each side. The lateral bands are continuous above with the inferior constrictor of the pharynx; the anterior arises from the back of the cricoid cartilage at the prominent ridge between the posterior crico-arytenoid muscles, and its fibres spreading out on each side of the gullet as they descend, soon blend with those of the lateral bundles to form a continuous layer around the tube. The direction of many of the fibres is at first slightly oblique, but towards the lower end it is more directly longitudinal. The internal or *circular* fibres are separated above by the fibres of the lateral longitudinal bands from those of the inferior constrictor of the pharynx. The rings which they form around the tube have a hori-

zontal direction at its upper and lower part, but in the intervening space are slightly oblique. At the lower end, both layers of fibres become continuous with those of the stomach.

The muscular coat of the upper end of the œsophagus is of a well-marked red colour, and consists wholly of striped muscular fibres ; but lower down, where it becomes somewhat paler, these are gradually replaced by plain muscular fibres, so that in the lower half of the tube the fibres are almost all of the involuntary kind. A few striped fibres, however, have been found mixed with the others throughout its whole length, and in many mammals the striped fibres preponderate throughout.

The longitudinal fibres of the œsophagus are sometimes joined by a broad band of smooth muscle, passing from the left pleura, and sometimes also by another from the left bronchus. According to Cunningham, the former is almost constantly present, and the latter very frequently.

The **areolar** or **submucous** coat is placed between the muscular and mucous coats, and connects them loosely together. It exceeds the mucous membrane considerably in thickness, and in it are contained the glands (fig. 510, *h*), which open on the mucous membrane.

The **mucous membrane** is of firm texture, and is paler in colour than that of the pharynx or stomach. From its loose connections its outer surface is freely movable on the muscular tunic ; and under ordinary circumstances the mucous lining is thrown into longitudinal folds or rugæ, which are in mutual contact. These folds disappear on distension of the canal.

Minute papillæ (*f*) are seen upon the mucous membrane, and the whole is covered with a thick stratified scaly epithelium. In the embryo for a certain period the œsophagus is lined by columnar ciliated epithelium (Neumann), patches of which may persist even to the time of birth (Klein).

The small compound racemose or tubulo-racemose glands, named *œsophageal glands*, which are for the most part seated in the submucous tissue (*i*), are especially numerous at the lower end of the tube. A few of the smallest are situated in the substance of the mucous membrane. In man the cells of these glands are columnar (Klein).

The mucous membrane is bounded next to the submucous coat by longitudinally disposed plain muscular fibres which, imperfect above, form a continuous layer towards the lower end of the tube (*muscularis mucosæ, e*).

Duplicity of the œsophagus in part of its extent, without other abnormality, has been recorded (Blaes, quoted by Meckel).

Vessels and nerves.—The *blood-vessels* of the œsophagus have for the most part a longitudinal arrangement. There are separate networks for the mucous membrane, the muscularis mucosæ and the muscular coat, and the glands and fat lobules which are met with in the submucosa have each their capillary plexus. *Lymphatics* are found in both the submucous and mucous coats, those of the latter commencing as in the mouth and pharynx within the papillæ. A small amount of lymphoid tissue is also present. Both here and in the pharynx the alveoli of the mucous glands are invested by sinus-like lymphatic vessels (Kidd). The *nerves* form a gangliated plexus between the two layers of the muscular coat, as in other parts of the alimentary canal, but it is characterised by the comparatively large size of the groups of ganglion-cells and of the cells themselves, and also by the fact that it contains a large number of medullated nerve-fibres (derived from the pneumo-gastric nerves). Each of these fibres in passing a ganglion is joined by a non-medullated fibre derived from one of the cells of the

ganglion, a T shaped junction being formed, as in the case of the large ganglia on the posterior roots of the spinal nerves. The medullated fibre then passes on, and after branching a certain number of times, is finally distributed in the muscular tissue in the striped fibres of which it terminates in the form of end-plates of the ordinary type (Ranvier). There is another nervous plexus in the submucous tissue.

Recent Literature.—*Gillette*, in Journ. de l'anat., 1872 (tunique musculaire); *Mouton*, in Rev. d. sci. méd., 1874 (calibre); *Cunningham*, in Journ. of Anat. and Phys., X., 1876; *Neumann*, in Arch. f. mikr. Anat., XII., 1876; *Klein*, in Qu. J. of micr. sci., XX., 1880; *Ranvier*, Leçons, 1880 (nerves and muscular coat).

THE ABDOMINAL VISCERA.

As that part of the digestive canal which is found beneath the diaphragm, and consists of the stomach and intestines, is situated within the cavity of the *abdomen*, and occupies, together with the liver, by far the greater part of that cavity, the general topographic relations of the abdominal viscera may here be briefly explained.

THE ABDOMEN.

The abdomen is the largest serous cavity in the body, and is lined by an extensive and complicated serous membrane, named the *peritoneum*. It extends from the diaphragm above to the levatores ani muscles below, and is subdivided into two parts: an upper and larger part, *the abdomen*, properly so called; and a lower or *pelvic* part. The limits between these portions of the cavity are marked by the brim of the true pelvis.

The enclosing walls of this cavity are formed principally of muscles and tendons which have been already described. They are strengthened internally by a layer of fibrous tissue lying between the muscles and the peritoneum, the different parts of which are described under the names of transversalis fascia, iliac fascia, and anterior layer of the lumbar aponeurosis. These walls are pierced by several apertures, through which are transmitted the great vessels and some other parts, such as the several diaphragmatic apertures for the aorta, vena cava and œsophagus, and the femoral arches and inguinal canals. In the median fibrous substance of the anterior wall lies the umbilical cicatrix. The cavity of the pelvis is also lined with strong fasciæ, and partially by peritoneum, and at its lower part are the apertures for the transmission of the rectum and the genito-urinary passages.

For the purpose of enabling reference to be made to the situation and condition of the contained organs, the *abdomen proper* has been artificially subdivided into certain regions, the boundaries of which are indicated by lines drawn upon the surface of the body. The description of these regions, together with an enumeration of their contents, has been given at the end of the first volume.

The surfaces of the viscera which are in contact one with another and with the wall of the cavity, are rendered glistening by a coating derived from the lining serous membrane of the cavity.

THE PERITONEUM.

The **peritoneum**, or serous membrane of the abdominal cavity, is by far the most extensive and complicated of the serous membranes. Like the others it may be considered to form a shut sac, but in the female, the two Fallopian tubes open at their free extremities into its cavity. The *parietal* layer is connected with the fascia lining the abdomen and pelvis

by means of areolar tissue (subperitoneal); it is more firmly adherent along the middle line of the body in front, as well as to the under surface of the diaphragm. The *visceral* layer, which is thinner than the other, affords a more or less complete covering to most of the abdominal and pelvic organs.

The *folds* of the peritoneum are of various kinds. Some of them, constituting the *mesenteries*, connect certain portions of the intestinal canal with the posterior wall of the abdomen; they are, the mesentery properly so called for the jejunum and ileum, the meso-cæcum, transverse and sigmoid meso-colon, and the meso-rectum. Other duplicatures exist, which are called *omenta;* they are the great omentum or epiloön, the small omentum, and the gastro-splenic omentum. Lastly, certain reflexions of the peritoneum from the walls of the abdomen or pelvis to viscera which are not portions of the intestinal canal, are named *ligaments:* such are the ligaments of the liver, spleen, uterus, and bladder.

The further account of the peritoneum will be deferred until the abdominal viscera have been described.

THE STOMACH.

The stomach is seated in the left hypochondriac and the epigastric regions. It lies in part against the anterior wall of the abdomen, and in part beneath the liver and diaphragm, and above the transverse colon. Its long axis, which is curved, is not horizontal in position, but lies obliquely, being considerably higher on the left side than on the right.

In **shape** it is somewhat conical or pyriform (fig. 511). The left extremity is the larger, and is named the *cardiac* end. The right or small end is named the *pyloric* extremity (*p*). Of its two orifices, the one by which food enters from the œsophagus is named the *cardiac* orifice (*o*), the other, by which it passes into the duodenum, and which is placed on a lower level, and more forwards, is the *pyloric* orific.

Fig. 511.

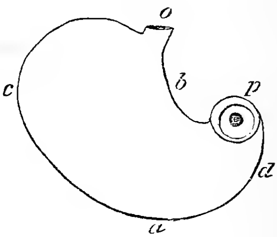


Fig. 511.—Diagrammatic outline of the stomach as seen from behind (His). $\frac{1}{4}$

a, great curvature; *b*, lesser curvature; *c*, left end, great cul-de-sac, or fundus; *d*, small cul-de-sac, or antrum pylori; *o*, œsophageal orifice or cardia; *p*, pyloric extremity.

The cardiac orifice is two or three inches from the larger extremity, which projects upwards and to the left of the opening, forming the great *cul-de-sac* or *fundus* (*c*).

Between the cardiac and the pyloric orifices, the outline of the stomach is curved along its upper and lower borders. The upper border, which looks also to the right, about three or four inches in length, is concave, and forms the *lesser* curvature (*b*); while the lower border, which is much longer, and, except towards the pylorus, convex, forms the *greater* curvature (*a*).

Towards the pylorus, the small end of the stomach describes a double bend, opposite to the first turn of which is a prominence or bulging, sometimes named the *small cul-de-sac* or *antrum pylori* (*d*).

There is sometimes a distinct constriction near the pyloric end of the stomach, imperfectly separating it into two parts. This condition may be in great

measure the result of local contraction of the muscular coat, but is occasionally of a more permanent character (Struthers).

When the stomach is distended, its position and direction are changed. The great curvature is elevated and at the same time carried forwards, whilst the anterior surface is turned upwards, and the posterior surface downwards.* The pylorus when the stomach is empty is nearly in the mesial plane of the body opposite the first lumbar to the eleventh dorsal vertebræ. When the stomach is distended the pylorus may be moved nearly three inches to the right (Braune).

The cardiac orifice is placed far back, in front and to the left of the body of the last dorsal vertebra.

Dimensions.—These vary greatly in different subjects, and also according to the state of distension of the organ. When moderately filled, its length is about 10 or 12 inches ; and its diameter at the widest part, from 4 to 5 inches. It weighs, when freed from other parts, about $4\frac{1}{2}$ ounces in the male, and somewhat less in the female (Clendinning). The wall of the stomach is thinner than that of the œsophagus, but thicker than that of the intestines generally. It is thickest at the pyloric end.

Connections.—The borders of the stomach are connected with folds of peritoneum in their whole extent. Thus, the superior border is connected with the under surface of the liver by a duplicature of peritoneum, the gastro-hepatic or lesser omentum, and at the left of the cardia, between the œsophagus and the diaphragm, is a small fold termed the gastro-phrenic ligament ; to the inferior border is attached the great omentum, beneath which is the transverse arch of the colon, while at the left extremity it is connected with the spleen by a duplicature of peritoneum, continuous with the left border of the great omentum, and named the gastro-splenic omentum or ligament. The blood-vessels and lymphatics of the stomach pass within these duplicatures of the membrane, and reach the organ along its two curvatures. Its anterior and posterior surfaces are free, smooth, and covered with peritoneum. The anterior surface which is directed upwards as well as forwards, is in contact above with the diaphragm and the under surface of the liver, and lower down with the abdominal parietes opposite the epigastric region, which is hence named the *pit of the stomach.* The posterior surface is turned downwards and backwards, and rests upon the transverse meso-colon, behind which are the pancreas, spleen, left kidney and supra-renal body, and the great vessels of the abdomen.

At its cardiac orifice it is continuous with the gullet, and is there fixed by reflection of the peritoneum to the œsophageal opening in the diaphragm. The pyloric extremity, situated lower down, nearer to the surface, and having greater freedom of motion, is continuous with the duodenum, is covered by the concave surface of the liver, and in some cases touches the neck of the gall-bladder.

STRUCTURE OF THE STOMACH.

The stomach has four coats, named, in order from without inwards, the serous, muscular, areolar or submucous, and mucous tunics (fig. 512).

The **external** or **serous coat** (*s*), derived from the peritoneum, is a thin, smooth, transparent, and elastic membrane which closely covers the entire viscus, excepting along its two curvatures. Along the line of these curvatures, the attachment is looser, leaving an interval occupied by the larger blood-vessels.

* This is denied by Lesshaft, who states that the general position of the stomach (which he describes as *vertical*) is unaltered by distension of the organ.

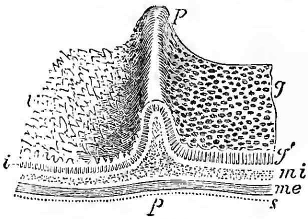
The second or **muscular coat,** is composed of plain muscular tissue, forming three sets of fibres, disposed in layers, and named, from their direction, the longitudinal, the circular, and the oblique fibres.

The first or outermost layer consists of the *longitudinal* fibres (fig. 512, *me*, fig. 513, A), which are in direct continuity with those of the œsophagus. They spread out in a radiating manner from the cardiac

Fig. 512.—DIAGRAMMATIC VIEW IN PERSPECTIVE OF A PORTION OF THE COATS OF THE STOMACH AND DUODENUM, INCLUDING THE PYLORUS (Allen Thomson).

g, the inner surface of the gastric mucous membrane ; *g′*, section of the mucous membrane with the pyloric gastric glands ; *v*, the villous surface of the mucous membrane of the duodenum : *i*, section of the same with the intestinal glands or crypts of Lieberkühn ; *p p*, the ridge of the pyloric ring, with a section of its component parts ; *m i*, deep or circular layer of muscular fibres : these are seen in the section to form the pyloric sphincter : *m e*, external or longitudinal layer of muscular fibres ; *s*, the serous covering.

Fig. 512.



orifice, and are found in greatest abundance along the curvatures, especially the lesser one. On the anterior and posterior surfaces they are very thinly scattered, or scarcely to be found, but towards the pylorus are well marked and form a thick uniform layer, which, passing over the pylorus, becomes continuous with the longitudinal fibres of the duodenum.

The second set consists of the *circular* fibres (fig. 512, *mi*, fig. 513, B) which form a complete layer over the whole extent of the stomach. They commence by small and thinly scattered rings at the left extremity of the great cul-de-sac, describe larger and larger circles as they surround the body of the stomach concentric to its curved axis, and towards the pyloric end again form smaller rings, and at the same time become much thicker and stronger than at any other point. At the pylorus itself they are gathered into an annular bundle (fig. 512 in section), which projects inwards into the cavity, and forms, within the annular fold of mucous membrane, the pyloric sphincter. Some of the circular fibres appear to be continued from those of the œsophagus, spreading from its right side.

The innermost muscular layer is incomplete, and consists of the *oblique* fibres (fig. 513, C). These are continuous with the circular fibres of the gullet, on the left of the cardiac orifice, where they form a considerable stratum ; from that place they descend obliquely upon the anterior and posterior surfaces of the stomach, where they spread out from one another, and taking the direction of the circular fibres gradually disappear on the greater curvature.

The **submucous coat** of the stomach is a distinct layer connecting the muscular and mucous coats (fig. 512, between *mi* and *g*). It consists of areolar tissue, in which occasional fat-cells may be found ; and it is the seat of division and passage of the blood-vessels.

The **internal coat** or **mucous membrane** is a smooth, soft, rather thick and pulpy membrane, which in the fresh state has generally a somewhat pink hue owing to the blood in its capillary vessels. In infancy the vascular redness is more marked.

The mucous membrane is thickest in the pyloric region, and thinnest in the great cul-de-sac. It always becomes thinner in old age.

Fig. 513.

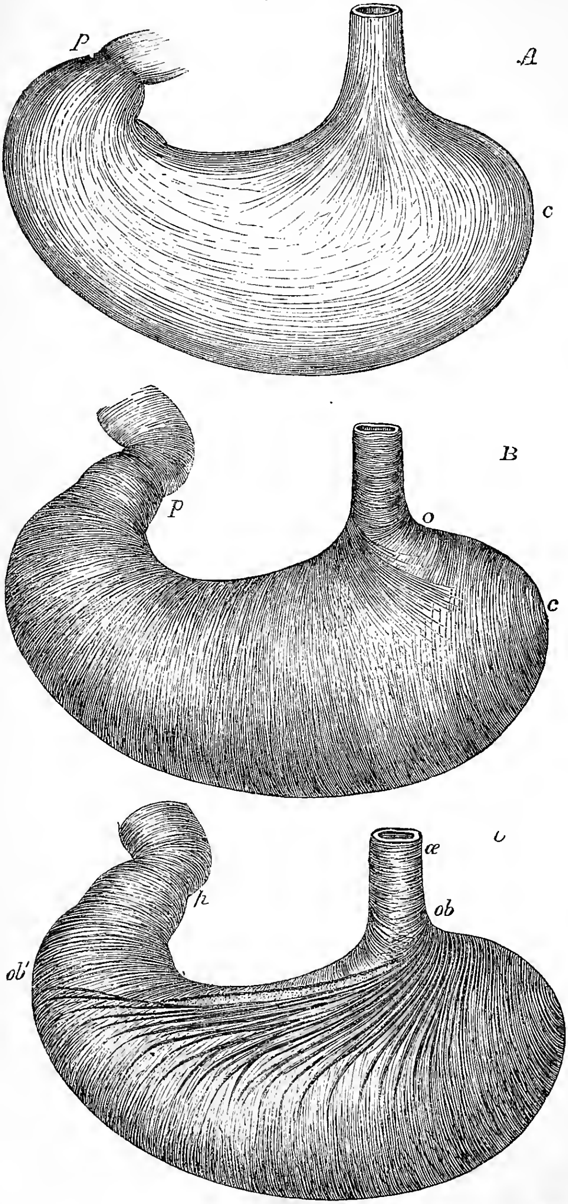


Fig. 513.—SKETCH OF THE ARRANGEMENT OF THE FIBRES IN THE MUSCULAR COAT OF THE STOMACH (Allen Thomson). $\frac{1}{3}$

A, external layer of longitudinal fibres, as seen from the outside; B, middle layer of circular fibres as seen on removing the longitudinal layer; C, oblique fibres exposed by removing some of the fibres of the circular layer, the cut edges of which are seen below the lesser curvature.

c, the cardiac end; *p*, the pyloric end; in A, are shown the stronger longitudinal fibres passing along the lesser and greater curvatures, and all round the pyloric end, and the radiating fibres spreading from the end of the gullet over the front (and back) of the stomach; in B, the nearly uniform layer of circular fibres, in two sets crossing each other very obliquely at *o*, and at the cardiac end becoming concentric to the centre of the great cul-de-sac; in C, the oblique fibres, *ob*, *ob′*, which form a continuation of the circular fibres of the gullet (*œ*) and spread from the left side of the cardia, gradually merging into the deeper circular fibres with which finally they entirely blend.

It is connected with the muscular coat by means of intervening sub-

mucous layer so loosely as to allow of considerable movement or displacement. In consequence of this, and of the want of elasticity of the mucous membrane, the internal surface of the stomach, when that organ is in an empty or contracted state, is thrown into numerous convoluted ridges, *rugæ*, which are produced by the wrinkling of the mucous, together with the areolar coat, and are entirely obliterated by distension of the stomach. These folds are most evident along the greater curvature, and have a general longitudinal direction.

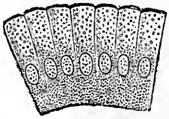
On examining the gastric mucous membrane closely with the aid of a simple lens, it is seen to be marked throughout, but more plainly towards the pyloric extremity, with small depressions which have a polygonal figure, and vary from about $\frac{1}{200}$th to $\frac{1}{100}$th of an inch across, being larger and more oblong near the pylorus. They are the enlarged mouths of the tubular glands with which the mucous membrane of the stomach is beset.

Towards the pyloric region of the stomach these depressions are larger and deeper, and their margins are elevated into pointed processes, which might be compared to rudimentary villi, but the perfect forms of those appendages exist only in the small intestine, and make their appearance in the duodenum, immediately beyond the pylorus.

Epithelium of the surface.—The thick stratified epithelium of the œsophagus passes abruptly at the cardia into a simple layer of columnar epithelium, which completely covers the inner surface of the stomach,

Fig. 514.—Epithelium of the surface of the stomach examined fresh (Heidenhain). Highly magnified.

Fig. 514.



and extends to a variable distance into the mouths of the gastric glands. The transition of the stratified into the columnar epithelium occurs quite suddenly, the lowermost columnar cells of the stratified epithelium passing into the single columnar layer of the gastric surface, and all the other layers of the stratified epithelium ceasing abruptly.

The epithelial cells of the surface of the stomach differ in some respects from the columnar epithelium of the intestine. They are more elongated in form, and in inactive conditions of the organ they exhibit two parts, the attached end of the cell being granular, the free part—that turned towards the inner surface of the organ—occupied by a clear, muco-albuminous substance (mucigen). Moreover, there is no striated border as in the intestinal cells. The clear substance swells and is discharged from the cell during digestion, leaving empty the part of the cell which contained it, and a similar change is produced by water and various other reagents. Between the smaller ends of the columnar cells, small, round or oval cells occur in greater or less number, sometimes in small nests (Watney).

Gastric glands.—As was first shown by Sprott Boyd, the surface of the stomach within the depressions above mentioned is dotted with small round apertures, which are the openings of minute glandular tubules, placed perpendicularly to the surface. On making a vertical section of the membrane, and submitting it to microscopic examination, it is seen to consist almost entirely of these small tubules, arranged parallel with each other. Each mouth or duct, together with the tubules which open into it, constitutes a *gastric gland.*

Some of the glands may be simple, consisting of a single tubule

throughout, but most are cleft into two or three tubules, or even, by the branching of these, eventually into six or eight. The glands have externally a basement membrane, composed of flattened cells joined edge to edge, and with processes which on the one side join the retiform tissue of the mucous membrane, and on the other side, more delicate, extend in amongst and support the enclosed epithelium cells.

Two kinds of glands are distinguished, which differ from one another both in the character of the enclosed cells, and, it is believed, in the nature of their secretion. Those of the one kind (fig. 515), are simpler in structure than the others, and being found most numerously in the pyloric region, they have been named *pyloric glands*. These are

Fig. 515.

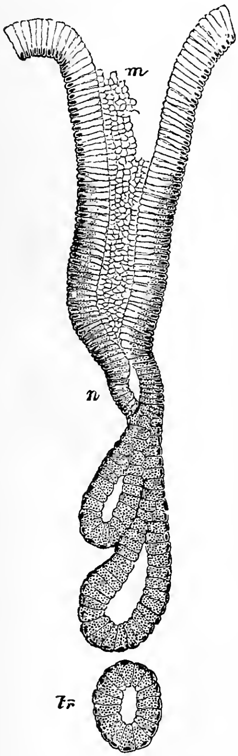


Fig. 515.—A PYLORIC GLAND, FROM A SECTION OF THE DOG'S STOMACH (Ebstein).

m, mouth ; *n*, neck ; *tr*, a deep portion of a tubule cut transversely.

distinguished by the large size and depth of the gland-mouth as compared with the tubules which open into it, and by the character of the epithelium lining the tubules. The mouth of the gland is lined throughout by an epithelium which is continuous with and similar to the columnar epithelium which covers the general surface of the stomach. But in the tubules of the gland the lining cells are shorter and more cubical, and are uniformly finely granular throughout ; moreover they are filled with secretion of a different nature from that of the surface epithelium.

Amongst the cells of these glands there are occasionally found others which are characterised by becoming darkly stained with osmic acid (Nussbaum). They were supposed to represent the parietal cells of the cardiac glands (see below), but this is probably not the case.

In the glands of the second kind (figs. 516, 517)—which may be termed from the portion of the stomach where they occur most numerously, the *cardiac glands* (fundus-glands of Heidenhain, oxyntic * glands of Langley)—the mouth, or part lined with epithelium like that of the surface, is comparatively short, and into it there open two, three or more tubules which are lined throughout and almost filled with short columnar or polyhedral cells ; these cells are in most respects similar to the secreting cells of the pyloric glands, but are much more coarsely granular. They were termed by Heidenhain the *principal cells* of the glands ; they are also known as the *central cells*. Between these cells and the basement membrane of the tubule other cells of a different

* From ὀξυς, acid ; since they contain the cells which produce the acid of the gastric secretion.

Fig. 517.

Fig. 516.

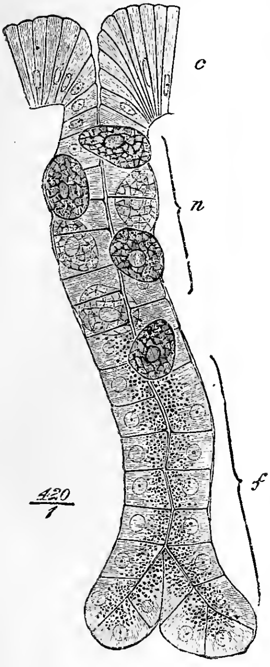


Fig. 516.—A CARDIAC GLAND OF SIMPLE FORM, FROM THE BAT'S STOMACH (Langley).

Osmic acid preparation.

c, columnar epithelium of the surface; *n*, neck of the gland with central and parietal cells; *f*, base or fundus, occupied only by principal or central cells, which exhibit the granules accumulated towards the lumen of the gland.

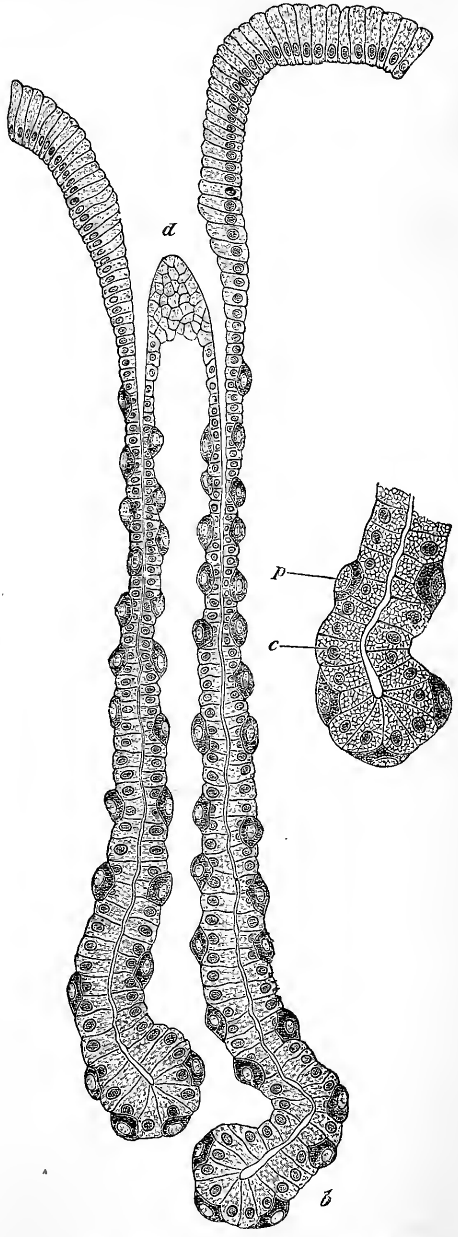


Fig. 517.—A CARDIAC GLAND FROM THE DOG'S STOMACH (Klein and Noble Smith). Highly magnified.

d, duct or mouth of the gland; *b*, base or fundus of one of its tubules. On the right the base of a tubule more highly magnified; *c*, central cell: *p*, parietal cell.

nature are interpolated in the cardiac glands. These are the *superadded, parietal* or *oxyntic cells.* They were long thought to be the only cells of the cardiac glands, and were on that account known as "peptic cells," a term which must now be entirely discarded.

The parietal cells are rather more closely arranged in the neck of the gland than elsewhere. They usually cease abruptly at the upper part of the neck, but occasional cells may be found under the columnar epithelium of the mouth or even of the general surface.

In some animals (porpoise, pig) the parietal cells lie each in a special pit formed by the basement membrane, and communicating with the rest of the gland only by a narrow orifice. In the glandular stomach of birds they line secondary tubules which lead out of the main tubule, this alone being lined by principal cells. In the frog and other amphibia the cardiac glands have only parietal or oxyntic cells, the principal cells being altogether absent, but glands containing cells which are similar in appearance and function to the principal cells of the stomach are found in the œsophagus.

The parietal cells have a finely granular appearance in the fresh condition, but in the gland hardened in alcohol are much darker and more granular looking. This appearance is due, according to Klein, not to the presence of actual granules within the cells, but to the existence of a close and uniform intracellular network (fig. 517). They are very readily stained by many colouring matters, especially by aniline blue.

The cells of the gastric glands undergo changes during the functional activity of the organ which are strictly comparable to the changes that have been described in the cells of the serous salivary glands. The principal cells of the cardiac glands—which during rest are in some animals granular throughout, and in others have a small outer zone clear of granules—become distinctly differentiated into two zones during activity, some of the granules becoming dissolved and discharged with the secretion, and the rest tending towards the lumen of the gland so as to leave the outer half or third of the cell clear of granules (fig. 516). After digestion has ceased the outer parts of the cells become again partially or wholly occupied by granules (Langley).

Both the central cells and the parietal cells undergo, according to Heidenhain, a change of size during digestion, becoming at first somewhat enlarged and subsequently shrinking to even less than their original volume. The changes occur a little later in the parietal than in the central cells.

The secreting cells of the pyloric glands undergo changes which are similar to those of the central cells of the cardiac glands.

Between the glands and at their base the mucous membrane consists of delicate connective tissue with retiform lymphoid tissue in small amount.

A thin layer of plain muscular tissue (*muscularis mucosæ*) bounds the mucous membrane externally, separating it from the submucous tissue. It consists of more than one stratum (an outer longitudinal and an inner circular), and is better marked in some animals than in man. Offsets pass from it between the gastric glands towards the surface of the mucous membrane.

Lymphoid follicles.—The stomachs of young persons sometimes present a mammillated aspect, due to little elevations of the surface, which are produced by local accumulations of lymphoid tissue, and somewhat resemble the solitary follicles of the intestine in appearance. The lymphoid accumulations in question are situated amongst the glands, and do not extend into the submucous tissue; they are not so distinctly circumscribed as those of the intestine, but fade off into the surrounding retiform tissue. They are most numerous at the junction of the stomach and small intestine (Watney).

Vessels and Nerves.—The stomach is a highly vascular organ. Its *arterial* branches, derived from all three divisions of the cœliac axis, reach the stomach between the folds of the peritoneum, and form, by anastomosing together, two principal arterial arches, which are placed along its two curvatures. After ramifying between the several coats and supplying them with blood (especially giving off numerous capillaries to the muscular coat) and after dividing into very small vessels in the submucous areolar tunic, the ultimate arterial branches (fig. 518, *a*) enter the mucous membrane, and ramifying freely, pass between the tubuli; here they form a plexus (*d*) of fine capillaries upon the walls of the tubules: and from this plexus larger vessels pass into a coarser capillary network around the mouths of the glands. The *veins*, fewer in number than the arteries, arise from the latter network, and take an almost straight course (*c*, *c*) through

Fig. 518.

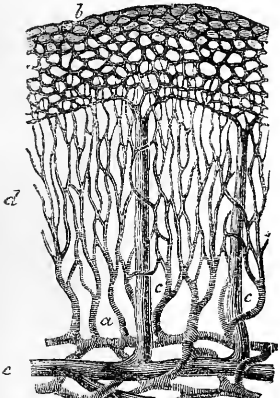


Fig. 519.

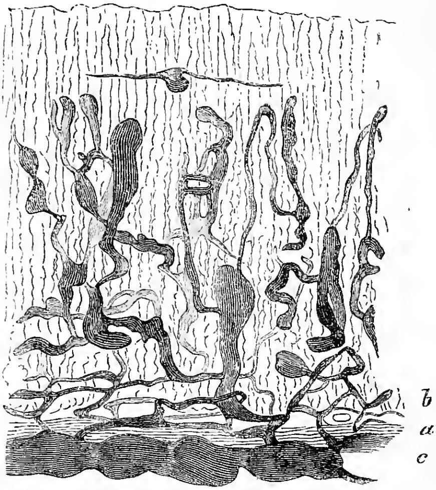


Fig. 518.—Plan of the blood-vessels of the stomach (from Brinton).

a, small arteries passing to break up into the fine capillary network, *d*, between the glands; *b*, coarser capillary network around the mouths of the glands; *c*, *c*, veins passing vertically downwards from the superficial network; *c*, larger vessels in the submucosa. The arteries in the deeper parts do not anastomose as here represented.

Fig. 519.—Lymphatics of the human gastric mucous membrane, injected (from Lovén).

The tubules are only faintly indicated; *a*, muscularis mucosæ; *b*, plexus of fine vessels at base of glands; *c*, plexus of larger, valved lymphatics in submucosa.

the mucous membrane between the glands. After piercing the muscularis mucosæ and forming a wide venous plexus in the submucous tissue, they return the residual blood into the splenic and superior mesenteric veins, and also directly into the vena portæ.

The *lymphatics* are very numerous. As shown by Lovén, they arise in the mucous membrane (fig. 519) by a dense network of lacunar spaces, situated between and amongst the gland-tubuli, which, as well as the blood-vessels, in many parts they enclose in sinus-like dilatations. Near the surface of the membrane the lymph is collected into vessels which form loops or possess dilated extremities; these vessels are less superficial than the blood-capillaries, although

the lacunar spaces extend as far as the basement membrane of the surface. At the deeper part of the mucous membrane the interglandular lymphatics pass into a plexus of fine vessels (*b*), immediately underlying the tubular glands; then piercing the muscularis mucosæ (*a*), they form a coarser, more deeply-seated network (*c*) in the submucous coat, the vessels of this network being provided with valves. Thence efferent lymphatics proceed and, piercing the muscular coats, follow the direction of the blood-vessels beneath the peritoneal investment, and traverse lymphatic glands found along the two curvatures of the stomach.

The *nerves*, which are large, consist of the terminal branches of the two pneumo-gastric nerves, belonging to the cerebro-spinal system, and of offsets from the sympathetic system, derived from the solar plexus. The left pneumo-gastric nerve descends on the front, and the right upon the back of the stomach. Numerous small ganglia have been found by Remak and others on both the pneumo-gastric and sympathetic twigs. The nerves form gangliated plexuses both between the layers of the muscular coat and in the submucous coat. Their ultimate ending has not been traced.

The pylorus.—While there is no special apparatus at the cardiac orifice of the stomach for closing the passage from the œsophagus, the opening at the pyloric end, leading from the stomach into the duodenum, is provided with a sphincter muscle. On looking into the pyloric end of the stomach, the mucous membrane is seen projecting in the form of a circular fold, called the *pylorus*, leaving a correspondingly narrow opening (fig. 533, *p*). Within this fold are circular muscular fibres, belonging to the general system of circular fibres of the alimentary canal, which are here collected in the form of a strong band, whilst the longitudinal muscular fibres and the peritoneal coat pass over the pyloric fold to the duodenum, and do not enter into its formation (fig. 512). Externally the pylorus may be easily felt, like a thickened ring, at the right end of the stomach, where also a slight external constriction is visible. Internally its opening is usually circular and less than half an inch across, so that it is the narrowest part of the whole alimentary canal.

Occasionally the orifice is oval, and it is often placed a little to one side. Sometimes the circular rim is imperfect, and there are found instead two crescentic folds, placed one above and the other below the passage (Huschke); and, lastly, there is occasionally but one such crescentic fold.

When the sphincter is contracted the longitudinal fibres covering it are bowed inwards, and these, if they contract at the same time that the sphincter muscle relaxes, will tend to dilate the orifice.

Recent Literature of the Stomach.—Form and position.—*Struthers*, in Monthly Journ. of Med. Sci., 1851, and Edinb. Med. Journ., 1861; *Betz*, in Viertelj. f. d. prakt. Heilk., 1873; *Braune* "Ue. d. Bewegl. d. Pylorus," Leipzig, 1873; *His*, in Arch. f. Anat. (u. Phys.), 1878; *Lesshaft*, Virch. Arch., LXXXVII., and Trans. of Intern. Med. Congress, 1881.—Structure.—*Heidenhain*, in Arch. f. mikr. Anat., VI. 1870, and article "Absonderung," in Hermann's Handbuch, 1880; *Ebstein*, in Arch. f. mikr. Anat., VI. 1870; *Klein*, in Stricker's Handbook, 1871; *Rollet*, in Graz Unters, 1871; *Lovén*, (lymphatics) in Nord. Med. Ark., 1873; *Biedermann* in Wiener Sitzungsb., 1875 (surface epithelium); *Watney*, in Phil. Trans., 1876; *Partsch*, in Arch. f. mikr. Anat., XIV. 1877, XVII. 1879; *Sewall* in Journ. of Physiol. I. 1878, (devel. of glands); *Nussbaum*; Arch. f. mikr. Anat., XVI. 1879; *Edinger*, *ibid.*, XVII. 1879; *Grützner*, in Pflüger's Arch., XX., 1879; *Langley and Sewall* in Journal of Physiol. II., 1879, and Proc. Roy. Soc., 1879; *Stöhr*, in Wurzb. Verhandl., 1880, and Arch. f. mikr. Anat., XX.; *Toldt*, in Wiener Sitzungsb., 1880 (dev. of glands); *Regéczky* in Arch. f. mikr. Anat., XVIII., 1880 (cilia on epithelium in some animals); *Langley*, Phil. Trans., 1881; and Journ. of Physiol. III., 1882.

THE SMALL INTESTINE.

The **small intestine** (fig. 520 D, J, I) commences at the pylorus, and after many convolutions terminates in the large intestine. It measures on an average about twenty feet in length in the adult, and gradually becomes slightly narrower from its upper to its lower end. Its convolutions occupy the middle and lower part of the abdomen, and are surrounded by the large intestine. They are connected with the back of the abdominal cavity, and are held in their position by a fold of the peritoneum, named the mesentery, and by numerous blood-vessels and nerves.

Fig. 520.

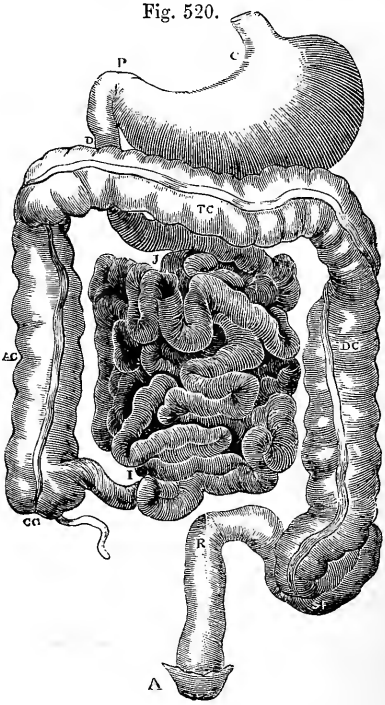


Fig. 520.—DIAGRAM OF THE ABDOMINAL PART OF THE ALIMENTARY CANAL (Brinton).

C, the cardiac, and P, the pyloric end of the stomach (this organ is represented in too horizontal a position); D, the duodenum; J, I, convolutions of the small intestine; CC, cæcum, with the vermiform process; AC, ascending, TC, transverse, and DC, descending colon; SF, sigmoid flexure; R, rectum; A, anus.

The small intestine is arbitrarily divided into three portions, which have received different names; the first ten or twelve inches immediately succeeding to the stomach, and comprehending the widest and most fixed part of the tube, being called the *duodenum*, the upper two-fifths of the remainder being named the *jejunum*, and the lower three-fifths the *ileum*. There are no distinct lines of demarcation between these three parts, but there are certain peculiarities of connection and certain differences of internal structure to be observed in comparing the upper and lower ends of the entire tube, which will be pointed out after it has been described as a whole.

STRUCTURE OF THE SMALL INTESTINE.

The small intestine, like the stomach, is composed of four coats, viz., the serous or peritoneal, muscular, areolar, and mucous.

The external or **serous coat** almost entirely surrounds the intestinal tube in the whole extent of the jejunum and ileum, leaving only a narrow interval behind, where it passes off and becomes continuous with the two layers of the mesentery. The line at which this takes place is named the *attached* or *mesenteric border* of the intestine. The duodenum, on the other hand, is but partially covered by the peritoneum.

The **muscular coat** consists of two layers of fibres; an outer longitudinal, and an inner or circular set. The *longitudinal* fibres constitute an entire but comparatively thin layer, and are most obvious along the free border of the intestine. The *circular* layer is thicker and more distinct.

The muscular tunic becomes gradually thinner towards the lower part of the small intestine. It is pale in colour, and is composed of plain muscular tissue, the cells of which are of considerable length. The progressive contraction of these fibres, commencing in any part of the intestine, and advancing in a downward direction, produces the peculiar *vermicular* or *peristaltic* movement by which the contents are forced onwards through the canal. In the narrowing of the tube the circular fibres are mainly concerned, the longitudinal fibres tending to produce dilatation (Exner); and those found along the free border of the intestine may have the effect of straightening or unfolding its successive convolutions.

The **submucous coat** of the small intestine is a layer of areolar tissue of a loose texture, which is connected more firmly with the mucous than with the muscular coat.

Fig. 521.

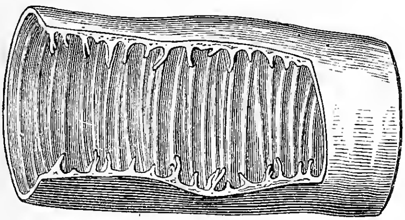


Fig. 521.—Portion of small intestine laid open to show the valvulæ conniventes (Brinton).

The internal coat or **mucous membrane**, is characterised by presenting all over its inner surface a finely flocculent or shaggy appearance, like the pile upon velvet, owing to its being thickly covered with minute processes, named *villi*. It is one of the most vascular membranes in the body, and is naturally of a reddish colour in the upper part of the small intestine, but is paler, and at the same time thinner, towards the lower end. It is lined with columnar epithelium throughout its whole extent, and next to the submucous coat is bounded by a layer of plain muscular tissue (*muscularis mucosæ*); between this and the epithelium the substance of the membrane, apart from the tubular glands which will be afterwards described, consists mainly of retiform tissue which supports the blood-vessels and lacteals, and encloses in its meshes numerous lymph-corpuscles.

In the lining membrane of the small intestine, however, there exist besides small effaceable folds or rugæ, other permanent ones, which cannot be obliterated, even when the tube is forcibly distended. These permanent folds are the **valvulæ conniventes**, or valves of Kerkring (fig. 521). They are crescentic projections of the mucous membrane, placed transversely to the axis of the bowel, each of them reaching about one-half or two-thirds of the distance round the interior of the tube, and they follow closely one upon another along the intestine. The largest are about $2\frac{1}{2}$ inches long and $\frac{1}{3}$ of an inch wide at the middle or broadest part.

Large and small valvulæ conniventes are often found to alternate with each other. Some of them are bifurcated at one end, and others terminate abruptly, appearing as if suddenly cut off. Each consists of a fold of the mucous membrane, that is, of two layers placed back to back, united together by the submucous areolar tissue. They contain no part of the circular or of the

longitudinal muscular coats. Being extensions of the mucous membrane, they serve to increase the absorbent surface to which the food is exposed.

There are no valvulæ conniventes quite at the commencement of the duodenum; a short distance from the pylorus they begin to appear; beyond the point at which the bile and pancreatic juice are poured into the duodenum they are very large, regularly crescentic in form and placed so near to each other that the intervals between them are not greater than the breadth of one of the valves; they continue thus through the rest of the duodenum and along the upper half of the jejunum; below that point they begin to get smaller and farther apart; and finally, towards the middle or lower end of the ileum, having gradually become more and more irregular and indistinct, sometimes even acquiring a very oblique direction, they altogether disappear.

Fig. 522.

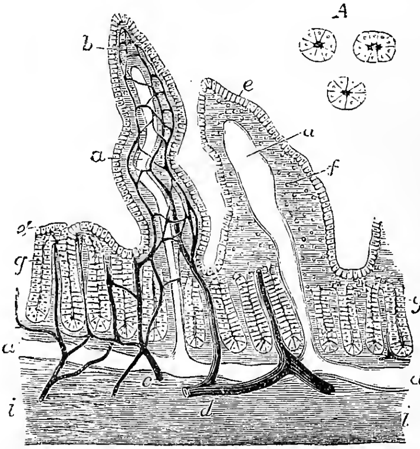


Fig. 522.—Vertical section of the intestinal mucous membrane of the rabbit (slightly altered from Frey). $\frac{150}{1}$.

Two villi are represented, in one of which the dilated lacteal alone is shown, in the other the blood-vessels and lacteal are both seen injected, the lacteal white, the blood-vessels dark: *a*, the lacteal vessels of the villi; *a'*, horizontal lacteal, which they join; *b*, capillary blood-vessels in one of the villi; *c*, small artery; *d*, vein; *e*, the epithelium covering the villi; *g*, tubular glands or crypts of Lieberkühn, some divided down the middle, others cut more irregularly; *i*, the submucous layer. A, cross section of three tubular glands more highly magnified.

The **villi,** peculiar to the small intestine, and giving to its internal surface the velvety appearance already spoken of, are small processes of the mucous membrane, which are closely set on every part of the inner surface over the valvulæ conniventes, as well as between them.

The villi are usually tapered and flattened in form in the human subject (fig. 523): some are cylindrical or finger-shaped (fig. 525), and have sometimes an enlarged or clubbed extremity. Occasionally two or three are connected together at their base.

Their length varies from $\frac{1}{50}$th to $\frac{1}{36}$th of an inch or sometimes more. They are largest and most numerous in the duodenum and jejunum, and become gradually shorter, smaller, and fewer in number in the ileum. In the upper part of the small intestine there are from 10 to 18 in a square millimeter, and in the ileum from 8 to 14 in the same space. This would give about 4 millions altogether (Krause).

A villus consists of a prolongation of the proper mucous membrane. It is covered by columnar epithelium (fig. 524), and encloses a network of blood-vessels, one or more lymphatic vessels (lacteals), and a few longitudinal plain muscular fibre-cells, these being all supported and held together by retiform lymphoid tissue. Under the epithelium is a basement membrane composed of flattened cells, which on the one hand are connected with the branched cells of the retiform tissue and on the other hand send processes between the epithelium-cells.

Nerves have not yet been demonstrated in the villi, although they are probably not wanting. Each villus receives, as a rule, one small *arterial* twig, which runs up the centre to near the middle of the villus, where it begins to break up into a number of capillaries (fig. 523). These form

Fig. 523.

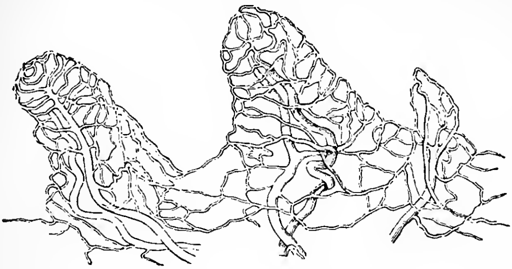


Fig. 523.—Magnified view of the blood-vessels of the intestinal villi.

The drawing was taken from a preparation injected by Lieberkühn, and shows, belonging to each villus, a small artery and vein with the intermediate capillary network.

near the surface, beneath the epithelium and limiting membrane, a fine capillary network, from which the blood is returned for the most part by a single *vein*, which in man commences near the tip of the villus, and passes through the mucous membrane into the submucosa without receiving lateral twigs. The general arrangement of the vascular supply of the villi varies considerably in different animals.

The lacteal lies in the centre of the villus (figs. 522, 524), and is in the smaller villi usually a single vessel, with a closed and somewhat

Fig. 524.

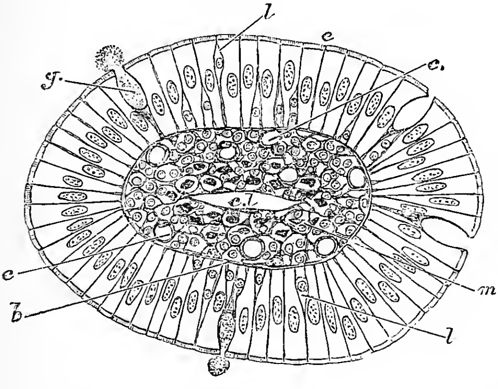


Fig. 524.—Cross section of a villus of the cat's intestine. (E.A.S.)

e, columnar epithelium; *g*, goblet cell, its mucus is seen partly exuded; *l*, lymph-corpuscles between the epithelium-cells; *b*, basement membrane; *c*, blood-capillaries; *m*, section of plain muscular fibres; *c.l*, central lacteal.

expanded extremity, and of considerably larger diameter than the capillaries of the blood-vessels around. According to the observations of Teichmann, there are never more than two intercommunicating lacteals in a single villus in the human subject (fig. 525, *b*); but both he and Frey found a copious network in the villi of the sheep. Like the lymphatics elsewhere, the lacteals in the villi are bounded by a delicate layer of flattened epithelial cells. These are connected with the branched cells and cell-spaces of the tissue of the villus, and these again with the flattened cells which form the basement membrane; from the latter, prolongations extend between the epithelium-cells towards the surface.

The muscular tissue within the villus was discovered by Brücke: it consists of a thin stratum of plain fibre-cells disposed longitudinally

around the lacteal; on being stimulated in animals, they produce an obvious retraction of the villus.

This muscular tissue is a prolongation from the muscularis mucosæ; the fibre-cells at the sides and towards the end of the villus pass from the lacteal to be attached to the basement membrane; usually their attachment to this is forked, a connective tissue corpuscle filling up the interval (Watney).

Fig. 525.

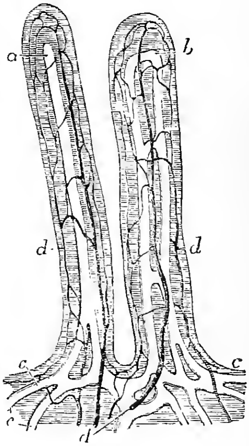


Fig. 525.—Injected lacteal vessels in two villi of the human intestine. 100 diameters (Teichmann).

The lacteals are represented as filled with white substance and the blood-vessels with dark. *a*, *b*, the lacteal vessels, single in one villus and double in the other; *c*, the horizontal lacteal vessels with which those of the villi communicate; *d*, the blood-vessels, consisting of small arteries and veins with capillary network between.

The columnar epithelium cells (figs. 526, 527), which cover not only the villi but also the rest of the surface of the intestine and extend into the tubular glands have already been described under the head of "Epithelium" (see pp. 43 to 45).

They are set upon the surface of the basement membrane often by a somewhat flattened extremity. I have never been able to detect any continuity between their attached extremity and the branched corpuscles of the retiform tissue of the villus, which has often been supposed to exist; on the contrary the epithelium separates with the greatest readiness from the subjacent tissue, and almost always with a simple truncated extremity, sometimes pitted but never much branched. (E.A.S.)

Amongst the ordinary epithelium-cells are others (fig. 524, *g*), the outer half of

Fig 526.

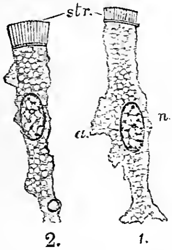


Fig. 527.

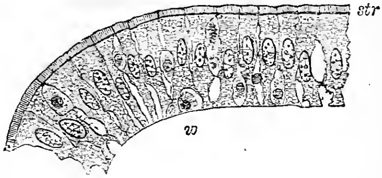


Fig. 526.—Columnar epithelium cells of the rabbit's intestine. (E. A. S.)

The cells have been isolated after maceration in very weak chromic acid. They are much vacuolated, and one of them (2) has a fat-globule near its attached end; the striated border (*str.*) is well seen, and the bright disk separating this from the cell-protoplasm; *n*, nucleus with intranuclear network; *a*, a thinned out wing-like projection of the cell which probably fitted between two adjacent cells.

Fig. 527.—A row of columnar cells from an intestinal villus of the rabbit. (E. A. S.)

str, striated border; *w*, smaller cells between the epithelium cells, probably of the nature of lymph-corpuscles.

which is filled with mucigen, and in some of these the mucus has become discharged from the cell, and the free end is ruptured (goblet-cells, see p. 44). The number

of cells containing mucus varies much in different animals and perhaps under different conditions in the same animal. There are comparatively few in the glands of the small intestine. During digestion of a meal containing fat the epithelial cells become turbid with minute oil-droplets in their interior; and at a subsequent stage branched cells within the tissue of the villus appear pervaded with similar fatty particles, and eventually the central lacteal becomes filled with them. There has been much difference of opinion as to the path taken by the fatty particles within the villus. It is possible that the amœboid lymph-corpuscles which are found so abundantly within the tissue of the villus, and even amongst the epithelium-cells of the surface, play an important part in the transference of the particles from the epithelium-cells to the lacteal; and the large amount of lymphoid tissue in the lower end of the small intestine may bear relation to a greater power of fat absorption in that part of the gut. In the transference of carbon particles in the lungs from the interior of the alveoli to the lymphatics, which at least in part is due to the activity of amœboid cells, we have an analogous process.

Other views which have been taken are (1) that the passage may occur through the branched connective tissue corpuscles of the villus, these being assumed to be in direct continuity with the fixed ends of the epithelial cells (which is certainly not the case). and (2) that the fat does not traverse the epithelium-cells at all, but passes wholly between them and is taken up by a fine *reticulum* (not a cell-network) which extend from the interspaces between the epithelium-cells through the tissue of the villus to be attached to the wall of the lacteal (Watney). There is, however, a difficulty in conceiving a mechanical explanation of the passage of the fat particles along the reticulum which Watney describes. It must be admitted that further investigations are necessary for the elucidation of this problem.

Glands.—Two kinds of small secreting glands open on the inner surface of the intestine, viz., the crypts of Lieberkühn, and Brunner's glands, the last being peculiar to the duodenum. In addition to these, numerous lymphoid nodules are found, which are either scattered and isolated (solitary glands) or collected into patches (Peyer's glands).

The **crypts of Lieberkühn,** the smallest but most numerous of these glandular structures, are found in every part of the small intestine, opening on the surface between the villi (fig. 522, *g*). They consist of

Fig. 528.

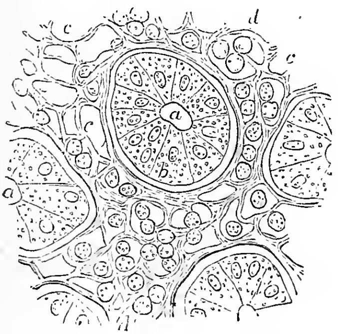


Fig. 528.—Lymphoid or retiform tissue of the intestinal mucous membrane of the sheep (from Frey). Magnified 400 diameters.

Cross section of a small fragment of the mucous membrane, including one entire crypt of Lieberkühn and parts of several others: *a*, cavity of the tubular glands or crypts; *b*, one of the lining epithelial cells; *c*, the lymphoid or retiform spaces, of which some are empty, and others occupied by lymph-cells as at *d*.

minute tubes, closed at their attached extremity which is slightly enlarged, and placed more or less perpendicularly to the surface, upon which they open sometimes two or three together. The crypts of Lieberkühn vary in length from the $\frac{1}{360}$th to the $\frac{1}{120}$th of an inch, and their diameter is about $\frac{1}{600}$th of an inch. They are longest in the duodenum. The walls of the tubes are formed of a basement membrane, lined with a columnar epithelium, (fig. 528).

Brunner's glands are small compound acino-tubular glands, which exist in the duodenum, where they are most numerous at the upper end, in general occupying thickly a space extending from one to two inches beyond the pylorus. A few of them are said also to be found quite at the commencement of the jejunum. They are imbedded in the submucous coat, and may be exposed by dissecting off the muscular coat from the outside of the intestine. In structure they somewhat resemble the small glands which are found in various parts of the lining membrane of the mouth and elsewhere, each consisting of a number of tubular alveoli, connected by the terminal ramifications of the duct, which latter penetrates the muscularis mucosæ, and opens upon the inner surface of the intestine. In sections through the pylorus the glands of Brunner appear like direct continuations of the pyloric glands of the stomach (Watney), which they closely resemble in structure, but are somewhat more complicated and more deeply seated.

The **solitary glands** are soft, white, rounded, and slightly prominent bodies about the size of a millet-seed, which are found scattered over the mucous membrane in every part of the small intestine. They are found as well at the mesenteric as at the free border, both between and upon the valvulæ conniventes, and are rather more numerous in the lower portion of the bowel. These so-called glands are in structure similar to the lymphoid nodules of various parts already described, consisting of clumps of dense retiform tissue, the meshes of which are closely packed with lymph-corpuscles and pervaded by fine capillaries. They are here and there united at the sides with the surrounding lymphoid tissue, but are at most points distinctly marked off from it, partly owing to the fact that their supporting retiform tissue becomes closer and finer, partly owing to their being surrounded by a rich plexus of lymphatic vessels; or they even hang, as it were, into a lymphatic (or lacteal) sinus, which may entirely surround the nodule, except next the inner surface of the intestine. The epithelium over the nodule often has a large number of lymph-corpuscles between the epithelial cells. The base of the nodule or follicle is situated in the submucous tissue; but it extends upwards, through the muscularis mucosæ, into the mucous membrane, causing a bulging of this towards the interior of the gut (as in fig. 531, *d d*). The prominent part of the follicle sometimes has villi upon it, and, placed around very irregularly, are seen the mouths of the crypts of Lieberkühn.

The **agminated glands** or **glands of Peyer** (who described them in 1677), are groups or patches of lymphoid nodules. The groups have an oblong figure (fig. 529), and vary from half an inch to two or even four inches in length, being about an inch, or rather less, in width: they are placed lengthways in the intestine at that part of the tube most distant from the mesentery; and hence, to obtain the best view of them, the bowel should be opened by an incision along its attached border.

The lymphoid nodules which by their aggregation make up a Peyer's patch are in almost all respects similar to the solitary glands above described. As a rule their surface is free from villi, and the crypts of Lieberkühn are collected in circles around them. Fine blood-vessels are distributed abundantly on the exterior of the follicles, and give off still finer capillary branches, which, supported by the retiform tissue, are disposed principally in lines converging to the centre (fig. 530).

The lacteal plexuses, which are abundant in the whole extent of the intestine, are especially rich where they surround the follicles of Peyer's glands (fig. 531), often forming sinuses around them, as in the case of the solitary follicles above described.

Fig. 529.

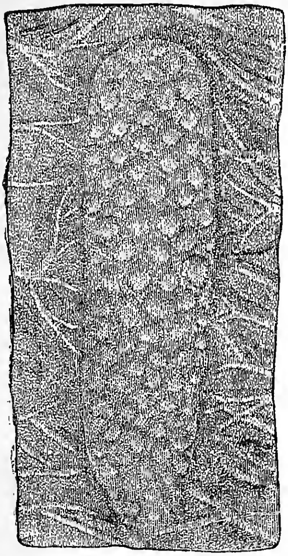


Fig. 529.—A small patch of Peyer's glands from the ilium. Slightly magnified (Bœhm).

In all, from twenty to thirty of these oblong patches may in general be found; but in young persons dying in health, as many as forty-five have been observed. They are larger and placed at shorter distances from each other in the lower part of the ileum; but in the upper portion of that intestine and in the lower end of the jejunum the patches occur less frequently, become smaller, and are of a nearly circular form; they may, however, be discovered occasionally in the lower portion of the duodenum. Still smaller irregularly shaped clusters of these follicles are sometimes found scattered throughout the intestine.

The glands of Peyer are best marked in the young subject. After middle life they become less obvious, and disappear almost completely in advanced age, their remains being often indicated by dark colouration of the mucous membrane.

Vessels and Nerves.—The branches of the mesenteric artery, having reached the attached border of the intestine, pass round its sides, dividing into numerous ramifications and frequently anastomosing at its free border. Most of the larger branches run immediately beneath the serous coat; they then pierce the muscular coat, supplying it with vessels as they pass, and ramify in the submucous areolar layer, so as to form a close network, from which still smaller vessels pass on into the mucous coat, and terminate in the capillary network of the folds, villi, and glands of that membrane. The fine

Fig. 530.

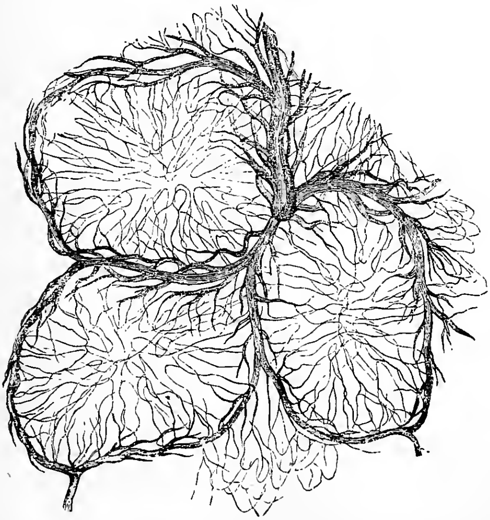


Fig. 530.—Portion of an injected Peyer's patch (from Kölliker). Magnified.

The drawing was taken from a preparation made by Frey of the intestine of the rabbit. It represents the fine capillary network spreading from the surrounding blood-vessels into the interior of three lymphoid nodules.

capillaries of the muscular coat are arranged in two layers of oblong meshes, which correspond in direction with the longitudinal and circular muscular fibres. The veins accompany the arteries.

The *lymphatics* of the intestine (lacteals) may be conveniently distinguished as those of the mucous membrane, and those of the muscular coat. Those of the mucous membrane form a copious plexus (fig. 531) which receives the central vessels of the villi and pervades both the mucous and submucous layers —in the latter being of considerable size, and forming, as before mentioned, a close plexus or a sinus around the base of each lymphoid follicle. Another set of lymphatics lies under the peritoneal coat, and is especially developed along a narrow strip at the attachment of the mesentery. In the muscular coat, the main plexus is situated between the circular and longitudinal layers of fibres (fig. 532, *l*); and there are likewise close plexuses threading the whole thickness of the muscular wall. These lymphatics of the muscular coat are in complete continuity with those of the mucous membrane, and pass into larger vessels at the mesenteric border, which again run into the lacteal vessels of the mesentery.

Fig. 531.

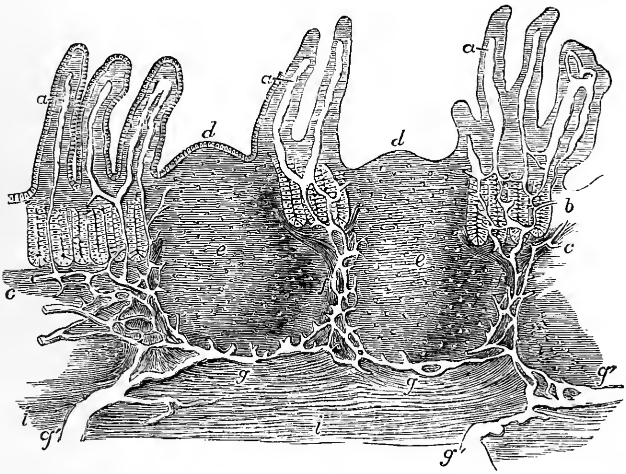


Fig. 531.—Vertical section of a portion of a patch of Peyer's glands, with the lacteal vessels injected (after Frey). 32 diameters.

The specimen is from the lower part of the ileum : *a*, villi, with their lacteals left white ; *b*, some of the tubular glands ; *c*, the muscular layer of the mucous membrane ; *d*, cupola or projecting part of the nodule ; *e*, their central part ; *f*, the reticulated lacteal vessels occupying the lymphoid tissue between the nodules, joined above by the lacteals from the villi and mucous surface, and passing below into *g*, the reticulated lacteals under the follicles, which again pass into the large, efferent lacteals, *g'* ; *i*, part of the muscular coat.

The *nerves* of the small intestine are chiefly derived from the superior mesenteric plexus. This plexus is formed by nervous branches, from the cœliac plexus, the semilunar ganglion, and from the vagus nerve. The plexus and plexiform branches into which it divides cling at first very closely to the larger divisions of the superior mesenteric artery, and, dividing similarly with the ramifications of the arteries, the branches of the nerves, retaining still a wide plexiform arrangement, pass onwards to the different parts of the intestine between the two folds of the mesentery, and finally, separating somewhat from the blood-vessels, reach the intestine in very numerous branches to be distributed in its coats. Passing first between the longitudinal and circular layer of the muscular coat, they here form a close gangliated plexus throughout the whole extent of

the intestine (fig. 532, *n*, as exhibited under a low power). This, which is known as the *plexus of Auerbach*, or the *plexus myentericus*, and which is principally composed of non-medullated fibres, gives off fine branches to the muscular substance; these first forming a smaller plexus amongst the muscular fibres. Other larger branches pass between the circular bundles of fibres to reach the submucous layer, where they form a second gangliated plexus (*plexus of Meissner*), the threads of which are much finer than those of the intermuscular plexus.

Fig. 532.

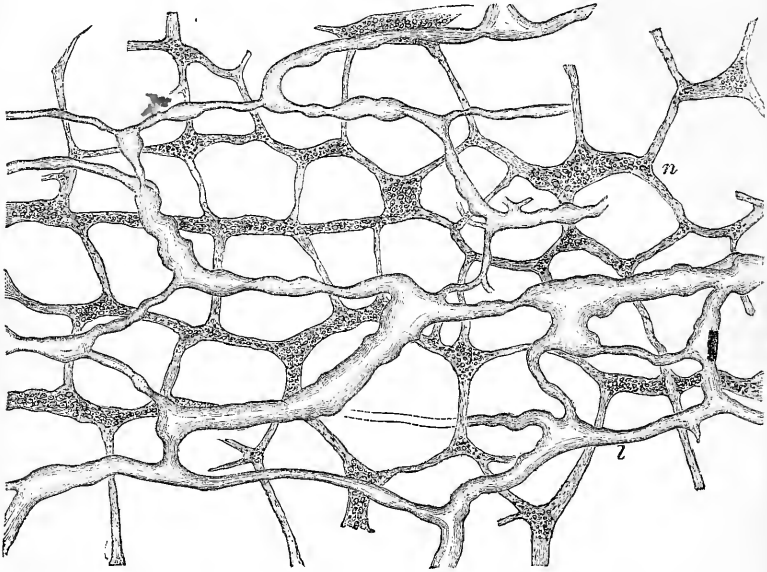


Fig. 532.—Lymphatic plexus (*l*) and nervous plexus (*n*) in the muscular coat of the intestine (Auerbach).

From Meissner's plexus nerve-fibres pass to be distributed to the muscular layer of the mucous membrane, breaking up into fine fibrils which take the direction of the fibre-cells of this layer, whilst other fine fibrils form a comparatively open plexus in the proper tissue of the mucous coat, and appear to send branches towards the epithelium, but the further course of these has not been traced.

SPECIAL CHARACTERS AND CONNECTIONS OF THE SEVERAL PARTS OF THE SMALL INTESTINE.

Duodenum.—This is the shortest and widest part of the small intestine. In length it measures about 10 inches, and in diameter it varies between 1½ and 2 inches. In its course it describes a single large curve of an almost circular shape but moulded over the front of the vertebral column (see fig. 550, p. 635) ; the termination in the jejunum being, in the empty condition of the stomach, only a little to the left of the commencement (Braune). The concavity embraces the head of the pancreas.

It has no mesentery, and is covered only partially by the peritoneum. Its muscular coat is comparatively thick, and its sub-mucous layer towards the pylorus is the seat of the glands of Brunner, already

described. The common bile-duct and the pancreatic duct open into this part of the intestinal canal.

Three portions of the duodenum are described by anatomists.

The first, or *superior* portion, about two inches long, extends from the pylorus upwards, backwards, and to the right, as far as beneath the neck of the gall-bladder, where it bends suddenly downwards. The first portion of the duodenum is for the most part moveable,

Fig. 533.

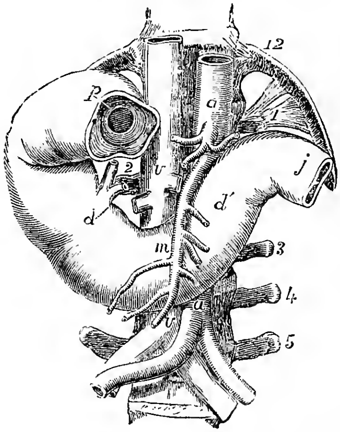


Fig. 533.—View of the duodenum from before (slightly altered from Luschka). $\frac{1}{4}$

12, the twelfth dorsal vertebra and rib ; 1, 3, 4, 5, transverse processes of the first, third, fourth, and fifth left lumbar vertebræ ; 2, that of the second on the right side ; *a*, *a*, the abdominal aorta above the cœliac axis and also near the bifurcation ; *m*, superior mesenteric artery ; *v*, *v*, the vena cava above the renal veins and near the bifurcation ; *p*, placed on the first part of the duodenum, points to the pyloric orifice seen from the side next the stomach, of which a small part is left connected with the intestine ; *d*, on the descending or second part of the duodenum, indicates the termination of the common bile-duct and the pancreatic duct ; *d'*, the third or oblique part of the duodenum ; *j*, the commencement of the jejunum. (This is represented as drawn over to the left, instead of curving forward as is actually the case.)

and invested by peritoneum like the stomach. Above, and in front of it, are the liver and gall-bladder, and it is commonly found stained by the exudation of bile from the latter a few hours after death. Behind it is the biliary duct, with the blood-vessels passing up to the liver.

The second, or *descending* portion, commencing at the bend below the neck of the gall-bladder, passes downwards as low as the second or third lumbar vertebra, where the bowel turns across to the left to form the third portion. This part of the duodenum is invested by the peritoneum on its anterior surface only,—the posterior surface being connected to the right kidney, the renal vessels and the vena cava by areolar tissue. In front is the transverse colon and mesocolon, which is continuous with the peritoneal covering of the duodenum. To the left is the head of the pancreas (see fig. 551, p. 635), which adapts itself to the shape of the intestine on that side, and, according to Verson, some of the longitudinal muscular fibres of the gut are intercalated amongst the contiguous lobules of the gland. The common bile-duct descends behind the left border of this part of the duodenum, and the pancreatic duct, accompanies it for a short distance. In the interior the valvulæ conniventes appear numerously ; and a downwardly projecting, papillary eminence of the mucous membrane is found immediately below one of these, about four inches below the pylorus, on the inner and back part of the intestine, at the apex of which is seen the common orifice of the biliary and pancreatic ducts.

The third, *transverse* or oblique portion (*d'*), somewhat the longest and narrowest, beginning on the right of the third lumbar vertebra, crosses in front of the second vertebra obliquely from right to left, finally making a

short turn to the right and forwards. It makes its appearance below the transverse mesocolon, and, continuing to ascend for an inch or more, ends in the jejunum (*j*) at the left side of the vertebral column, immediately behind the root of the transverse mesocolon, and the commencement of the mesentery, these being covered by the stomach. It has the vena cava inferior and the aorta behind it, while in front of it the superior mesenteric vessels (*m*) pass from beneath the pancreas to enter the mesentery.

At its termination the duodenum turns abruptly forwards to be continued into the jejunum. It is maintained, at that point, in its position, by a strong fibrous band descending from the left crus of the diaphragm and the tissue around the cœliac axis. According to Treitz, plain muscular fibres come from both these sources to this part of the duodenum. In subjects in which the intestines are large and dilated, the curve of the duodenum may descend to the level of the iliac crest, but, owing to the support given by the band alluded to, its terminal extremity maintains a uniform position.

Jejunum and Ileum.—The *jejunum*, originally so called from its having been supposed to be empty after death, follows the duodenum, and includes the upper two-fifths of the remainder of the small intestine, while the succeeding three-fifths constitute the *ileum*, so named from its numerous coils or convolutions. Both the jejunum and the ileum are attached and supported by an extensive fold of peritoneum termed the *mesentery*. The mesentery of the small intestine, although greatly frilled out in front to correspond in length with the jejunum and ileum to which it affords support, is attached posteriorly by a very short border which extends from the level of attachment of the transverse colon immediately to the left of the middle line, directly down to the right iliac fossa, where the ileum falls into the cæcum. At its widest part the length of the mesentery is from four to six inches between its vertebral and its intestinal border. Between the two layers of peritoneum of which it consists, are placed, besides some fat, numerous branches of the superior mesenteric artery and vein, together with nerves, lacteal vessels, and mesenteric glands. The convolutions of the jejunum are situated in part of the umbilical and left lumbar and iliac regions of the abdomen; while the ileum occupies part of the umbilical and right lumbar and iliac regions, together with the hypogastric, and its lower part descends into the pelvis supported by a short mesentery. From here it ascends obliquely to the right and somewhat backwards, over the corresponding psoas muscle, and ends in the right iliac fossa, by opening into the inner side of the commencement of the large intestine. The character of the intestine gradually changes from its upper to its lower end, so that portions of the two intestines, remote from each other, present certain well-marked differences of structure. Thus, the ileum is narrower; its coats are thinner and paler; the valvulæ conniventes are small, and gradually disappear towards its lower end; the villi are shorter; and the groups of Peyer's glands are larger and more numerous. The diameter of the jejunum is about one inch and a half, that of the ileum about one inch and a quarter. A given length of the jejunum weighs more than the same of the ileum.

At a point in the lower part of the ileum it is not very uncommon to find a pouch or *diverticulum* given off from the main tube. The origin of these

diverticula is probably connected with the persistence of a part of the vitelline duct of early fœtal life. They are not to be confounded with hernial protrusions of the mucous membrane, which may occur at any point.

Recent Literature of the small Intestine.—*Verson*, in Stricker's Handbook, 1871; *Heller*, in Ber. d. Sachs. Gesellsch., 1872 (blood-vessels); *Schwalbe*, in Arch. f. mikr. Anat., VIII., 1872 (Brunner's glands); *Heidenhain*, in Arch. f. mikr. Anat., VIII., 1872 (Brunner's glands), and article in Hermann's Handb., 1881; *Thannhofer*, in Pflüger's Arch., VIII., 1873, and Med. Centralbl., 1876 (fat absorption); *H. Watney*, in Med. Centralbl., 1874, and Phil. Trans., 1876 (structure of alimentary canal, and fat absorption); *Defois*, in Rev. d. sci. méd., 1874 (vessels); *Grützner*, in Pfluger's Arch., 1876 (Brunner's glands); *Winiwarter*, in Wiener Sitzungsb., 1876 (lacteals); *Exner*, in Wiener Sitzungsb., 1877 (action of longit. muscles); *Klose*, Dissert., Breslau, 1880 (crypts of Lieberkühn); *Hoffmann*, Dissert., München, 1878 (solitary glands).

THE LARGE INTESTINE.

The large intestine extends from the termination of the ileum to the anus. It is divided into the cæcum (with the vermiform appendix), the colon and the rectum; and the colon is again subdivided, according to its direction, into four parts, called the ascending, transverse, and descending colon, and the sigmoid flexure (fig. 520).

The length of the large intestine is usually about 5 or 6 feet; being about one-fifth of the whole length of the intestinal canal. Its diameter, which for the most part greatly exceeds that of the small intestine, varies at different points from two inches and a half to about one inch and a half. It diminishes gradually from its commencement at the cæcum to its termination at the anus; excepting that there is a well-marked dilatation of the rectum just above its lower end.

In outward form, the greater part of the large intestine differs remarkably from the small intestine; for, instead of constituting an even cylindrical tube, its surface is thrown into numerous sacculi, marked off from each other by intervening constrictions, and arranged in three longitudinal rows, separated by three strong flat bands of longitudinal muscular fibres. This sacculated structure is not found in the rectum.

Fig. 534.

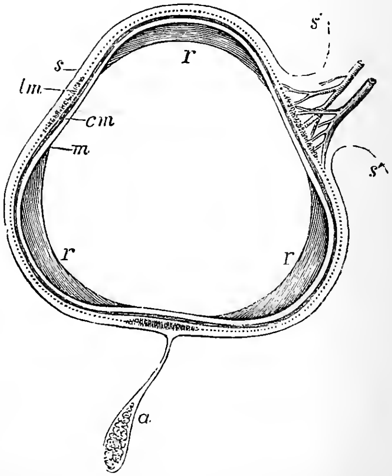


Fig. 534.—Outline sketch of a section of the ascending colon (Allen Thomson). $\frac{3}{4}$

s, serous covering; *s′*, *s′*, reflection of this at the attached border forming a short wide mesentery, between the folds of which the blood-vessels are seen passing to the colon; *a*, one of the appendices epiploicæ hanging from the inner border; *l m*, indicates at the free border one of the three bands formed by the thickening of the longitudinal muscular coat; the dotted line continued from the margins of these bands represents the remainder of the longitudinal muscular coat, and the thick line within it marked *c m*, represents the circular muscular layer; *m*, the mucous membrane at the flattened part; *r*, the crescentic bands or indentations which divide the sacculi.

STRUCTURE OF THE LARGE INTESTINE.

The large intestine has four coats, like those of the stomach and small intestine, namely, the serous, muscular, submucous, and mucous.

The **serous coat** is for the most part similar to that of the small intestine, except that, along the colon and upper part of the rectum, it is prolonged into numerous little projections, which enclose a certain amount of fat, and are termed *appendices epiplöicæ.*

Fig. 535.

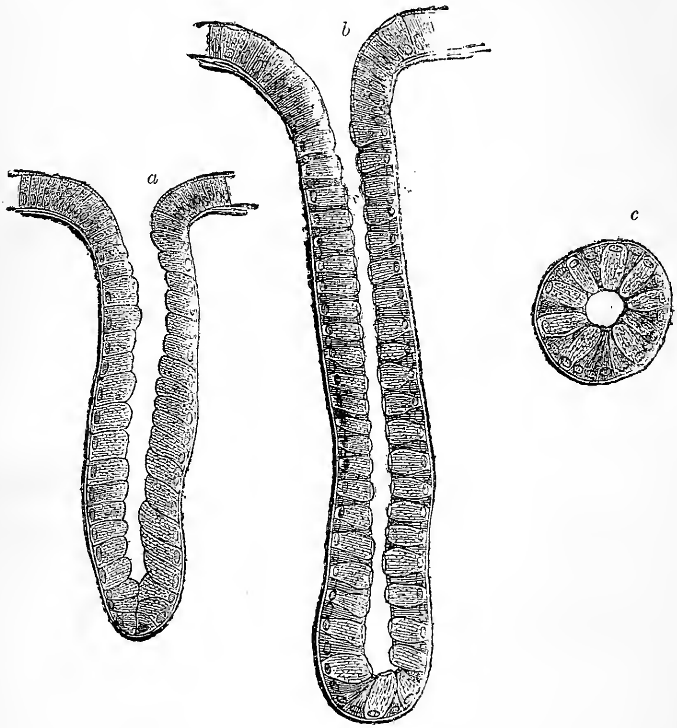


Fig. 535.—Glands of the large intestine. Magnified (from Heidenhain and Klose).

a, of the rabbit; *b*, of the dog. *c*, transverse section of a gland of the dog.

The **muscular coat,** like that of the other parts of the intestinal canal, consists of external longitudinal and internal circular fibres.

The *longitudinal* fibres, although found in a certain amount all round the intestine, are, in the cæcum and colon, more thickly collected into three remarkable flat longitudinal bands (fig. 534, *l m*; fig. 520). These bands, sometimes called the ligaments of the colon, are about half an inch wide, and half a line thick; they commence upon the extremity of the cæcum, at the attachment of the vermiform appendix, and may be traced along the whole length of the colon as far as the commence-

ment of the rectum, where they spread out, so as to surround that part of the intestinal tube with a uniform layer of longitudinal muscular fibres. One of these bands, the *posterior*, is placed along the attached border of the intestine; another runs along its *anterior* border, and, in the transverse colon, corresponds with the attachment of the great omentum; whilst the third band (*inner*) is found on the inner border of the ascending and descending colon, and on the under border of the transverse colon. It is along the course of this third band that the appendices epiploicæ are most of them attached (fig. 534, *a*). Measured from end to end, these three bands are shorter than the intervening parts of the tube; and the latter are thus thrown into the sacculi already mentioned: accordingly, when the bands are removed by dissection, the sacculi are entirely effaced, and the colon, elongating considerably, assumes the cylindrical form. The transverse constrictions seen on the exterior of the intestine, between the sacculi, appear on the inside as sharp ridges separating the cells, and are composed of all the coats. In the vermiform appendix the longitudinal muscular fibres are disposed in a uniform layer.

The *circular* muscular fibres form only a thin layer over the general surface of the cæcum and colon, but are accumulated in larger numbers between the sacculi. In the rectum, especially towards its lower part, the circular fibres form a very thick and powerful muscular layer.

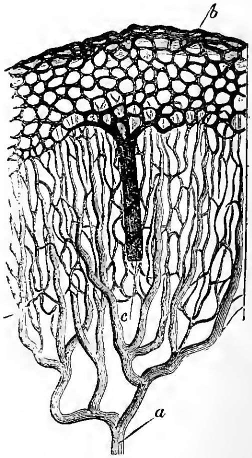
The **submucous** or **areolar** coat resembles in all respects that of the small intestine.

The **mucous membrane** differs from that of the small intestine in

Fig. 536.—Blood-vessels of large intestine as seen in vertical section (Kölliker).

a, artery passing up from submucosa; *c*, vein arising from capillary plexus, *b*, which surrounds the mouths of the glands.

Fig. 536.



being smooth and destitute of villi. Viewed with a lens, its surface is seen to be marked all over by the orifices of numerous tubular glands (*crypts of Lierberkühn*) (fig. 535), resembling those of the small intestine, but longer and more numerous, and further distinguished from them by the large number of mucus-cells which they contain. Indeed in some animals all the cells of these glands may be found to be filled with mucus (fig. 535, *a*); in others every alternate cell presents this character, the cells between being of the ordinary columnar kind.

If the glands are stimulated to active secretion the mucus is discharged and all the cells assume the appearance of ordinary columnar epithelium-cells (Klose).

Scattered over the whole large intestine *lymphoid nodules* are found, similar to the solitary glands of the small intestine, but less prominent.

They are most numerous in the cæcum and its vermiform appendix; being placed closely all over the latter.

The epithelium which covers the general surface of the mucous membrane is of the columnar kind, and in every respect similar to that of the small intestine. As in the stomach the mucous membrane consists of areolar connective tissue with a certain amount of retiform tissue, and is bounded next the submucous coat by a layer of plain muscular fibres (*muscularis mucosæ*), which sends prolongations up between the glands to be attached to the basement membrane near the surface, in the same way as in the villi of the small intestine.

Vessels and Nerves.—In the large intestine an arrangement of capillary plexuses and venous radicles obtains, similar to that which has been described in the stomach (fig. 536). The arrangement of the lymphatics is also nearly the same.

Nervous plexuses similar to those of the small intestine are also found in the muscular and submucous coats of the large intestine.

SPECIAL CHARACTERS AND CONNECTIONS OF THE DIFFERENT PARTS OF THE LARGE INTESTINE.

The Cæcum.—The *intestinum cæcum*, or *caput cæcum coli*, is that part of the large intestine which is situated below the entrance of the ileum (fig. 520, CC). Its length is about 2½ inches, and its diameter nearly the same: it is the widest part of the large intestine.

The cæcum is situated in the right iliac fossa, immediately behind the anterior wall of the abdomen. It is covered by the peritoneum in front, below, and at the sides: but behind it is usually destitute of peritoneal covering, and is attached by areolar tissue to the fascia covering the right iliacus muscle. In this case the cæcum is comparatively fixed; but in other instances the peritoneum surrounds it almost entirely and forms a duplicature behind it, called *meso-cæcum.*

Coming off from the inner and back part of the cæcum, at its lower end, is a narrow, round, and tapering portion of the intestine, named the *appendix cæci*, or **vermiform appendix**. The width of this process is usually about that of a large quill or rather more, and its length varies from 3 to 6 inches, these dimensions differing much in different cases. Its general direction is upwards and inwards behind the cæcum; and after describing a few slight turns it ends in a blunt point. It is retained in its position by a small fold of peritoneum, which forms its mesentery. The cæcal appendix is hollow as far as its extremity: and its cavity communicates with that of the cæcum by a small orifice, sometimes guarded by a valvular fold of mucous membrane.

So far as is known, this appendix is peculiar to man and certain of the higher apes, and to the wombat; but in some animals, as in the rabbit and hare, the distal part of the cæcum, being diminished in diameter and thickly studded with lymphoid follicles, may represent a condition of the appendix.

Ileo-cæcal or **ileo-colic valve.**—The lower part of the small intestine (fig. 537, *i*), ascending from left to right, and from before backwards, enters the commencement of the large intestine with a considerable degree of obliquity about 2½ inches from the blind end of the cæcum. The opening leading from the ileum into the large intestine is guarded

by a valve composed of two segments or folds. This is the *ileo-cæcal* or *ileo-colic valve:* it is also called the valve of Bauhin and the valve of Tulpius, although Fallopius had described it before either of those anatomists.

The ileum communicates with the colon by a narrow elongated slit-like aperture, lying nearly transversely to the direction of the large intestine.

Fig. 537.

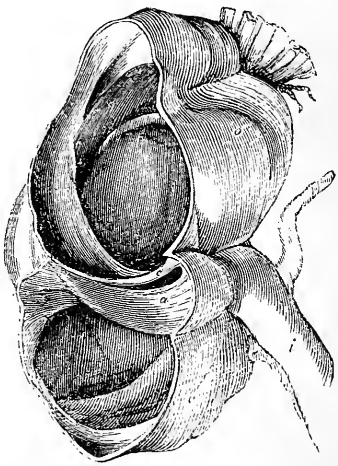


Fig. 537.—View of the ileo-colic valve from the large intestine (after Santorini). ½

The figure shows the lowest part of the ileum, *i*, joining the cæcum, *c*, and the ascending colon, *o*, which have been opened anteriorly, so as to display the ileo-colic valve; *a*, the lower, and *e*, the upper segment of the valve.

The aperture is rounded and widened at its anterior end which is turned slightly to the left, but the posterior end is narrow, and pointed. It is bounded above and below by two prominent semilunar folds, which project inwards towards the cæcum and colon. The upper of these (fig. 537, *e*) is horizontal, the lower and larger (*a*) slightly oblique. At each end of the aperture these folds coalesce, and are then prolonged as a single ridge on each side for some distance round the cavity of the intestine, forming the *fræna* or *retinacula* of the valve. The opposed surfaces of the valvular folds which look towards the ileum, and are continuous with its mucous surface, are covered like it with villi; while their other surfaces, turned toward the large intestine, are smooth and destitute of villi. When the cæcum is distended, the fræna of the valve are stretched, and the marginal folds brought into apposition, so as completely to close the aperture and prevent reflux into the ileum, while at the same time no hindrance is offered to the passage of additional matter from thence into the large intestine.

Each segment of the valve consists of two layers of mucous membrane, continuous with each other along the free margin, and including between them, besides the submucous areolar tissue, a number of muscular fibres, continued from the circular fibres of the ileum and of the large intestine. The longitudinal muscular fibres and the peritoneal coat take no part in the formation of the valve, but are stretched across it uninterruptedly from one intestine to the other.

The Colon.—The ascending colon, situated in the right lumbar and hypochondriac regions, commencing at the cæcum opposite to the ileo-cæcal valve, ascends vertically to the under surface of the liver, near the gall-bladder, where it proceeds forwards and then turns abruptly to the left, forming what is named the *hepatic flexure* of the colon. The ascending colon is smaller than the cæcum, but larger than the trans-

verse colon. It is overlaid in front by some convolutions of the ileum, and is bound down firmly by the peritoneum, which passes over its anterior surface and its sides, and generally leaves an interval in which its posterior surface is connected by areolar tissue with the fascia covering the quadratus lumborum muscle, and with the front of the right kidney. In some cases, however, the peritoneum passes nearly round it, and thus forms a distinct though very short meso-colon.

The TRANSVERSE COLON describes an arch, the convexity of which is turned towards the anterior abdominal wall; and it has accordingly been named the *arch of the colon.* It passes across from the right hypochondrium, through the upper part of the umbilical region, into the left hypochondrium. Sometimes it is found as low as the umbilicus or even lower. At each extremity it is situated deeply towards the back part of the abdominal cavity, but in the middle it curves forwards, and lies close to the anterior wall of the abdomen.

Above, the transverse colon is in contact with the under surface of the liver, the gall-bladder, the great curvature of the stomach, and the lower end of the spleen. Below it are the convolutions of the small intestine, the third portion of the duodenum being behind it. It is invested by the general peritoneum, which forms a separate fold for it, the *transverse meso-colon,* and in front it adheres to the lower fold of the sac of the omentum.

The DESCENDING COLON is continuous with the left extremity of the transverse colon by a sudden bend named the *splenic flexure.* At this bending there is found a remarkable fold of peritoneum, the *costo-colic* or *pleuro-colic ligament,* which stretches with a lunated free border to the colon from the diaphragm, opposite the 10th or 11th rib. As was pointed out by Haller, it supports the spleen although unconnected with that organ, and might be termed "sustentaculum lienis." The colon then descends almost perpendicularly through the left hypochondriac and lumbar regions to the left iliac fossa, where it ends in the sigmoid flexure. The peritoneum affords a covering to it only in front and at the sides, whilst behind it is connected by areolar tissue to the diaphragm, the quadratus lumborum, and the left kidney. It is usually concealed behind some convolutions of the jejunum.

The SIGMOID FLEXURE of the colon, situated in the left iliac fossa, consists of a double bending of the intestine upon itself in the form of the letter S, immediately before it becomes continuous with the rectum at the margin of the pelvis opposite to the left sacro-iliac articulation. It is attached by a distinct meso-colon to the iliac fossa, and is very movable, falling into the pelvis when the bladder is empty. It is placed immediately behind the anterior wall of the abdomen, or is concealed only by a few turns of the small intestine. The sigmoid flexure is the narrowest part of the colon.

THE RECTUM.—The lowest portion of the large intestine, named the *rectum,* extends from the sigmoid flexure of the colon to the anus, and is situated entirely within the true pelvis, in its back part (fig. 538, *r, r*).

Commencing opposite the left sacro-iliac articulation, it is directed at first obliquely downwards, and from left to right, to gain the middle line of the sacrum. It then changes its direction, and curves forwards in front of the lower part of the sacrum and the coccyx, and behind the bladder, vesiculæ seminales and prostate in the male, and at the back of the cervix uteri and vagina in the female. Opposite the

prostate it makes another turn, and inclines downwards and backwards to reach the anus. Seen from the front, the upper part of the rectum presents a lateral inclination from the left to the median line of the pelvis, sometimes passing beyond the middle to the right ; and when viewed from the side (fig. 538), it offers two curves, one corresponding

Fig. 538.

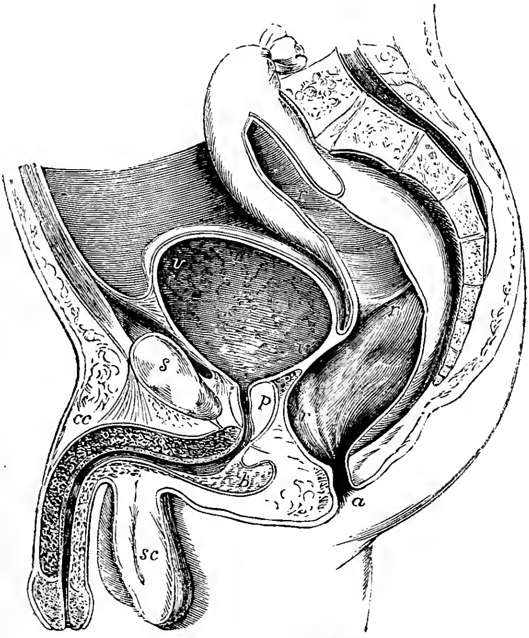


Fig. 538.—Vertical section of the pelvis and its viscera in the male (Allen Thomson, after Houston). $\frac{1}{3}$

This figure is introduced to illustrate the form, position, and relations of the rectum ; it also shows the bladder and urethra with the pelvic inflection of the peritoneum over these viscera : *r*, *r'*, *r'*, the upper and middle parts of the rectum, and at the middle letter the fold separating the two ; *r'*, *a*, the lower or anal portion ; *v*, the upper part of the urinary bladder ; *v'*, the base, at the place where it rests more immediately on the rectum ; *p*, the prostate gland and prostatic portion of the urethra ; *b*, the bulb ; *c*, *c*, the corpus cavernosum penis and suspensory ligament ; *sc*, the scrotum ; *s*, symphysis pubis.

with the hollow front of the sacrum and coccyx, and the other at the lower end of the bowel, forming a shorter turn in the opposite direction.

The *intestinum rectum*, therefore, so called from its original description being derived from animals, is far from being straight in the human subject.

Unlike the rest of the large intestine, the rectum is not sacculated, but is smooth and cylindrical ; and it has no separate longitudinal bands upon it. It is about eight inches in length, and at its upper end is rather narrower than the sigmoid flexure, but becomes dilated into a large ampulla or reservoir immediately above the anus.

The upper part of the rectum, covered by peritoneum, is in contact in front with the back of the bladder (or uterus in the female), unless some convolutions of the small intestine happen to descend between them. The ureter and branches of the internal iliac artery are in contact with it on the left side. It is attached behind to the sacrum by a duplicate of peritoneum named the *meso-rectum*. Lower down the peritoneum covers the intestine in front and at the sides, and at last in front only; still lower, it quits the intestine altogether, and is reflected forwards to ascend in the male upon the back of the bladder, in the female on the back of the upper part of the vagina and the uterus. In passing from the rectum to the bladder, the peritoneum forms a cul-de-sac, the recto-vesical pouch, which extends downwards between the intestine and the bladder to within an inch or more from the base of the prostate, and is bounded above at each side by a lunated fold of the serous membrane, of which the left is almost always the larger (posterior ligaments of the bladder).

Below the point where the peritoneum ceases to cover it, the rectum is connected to surrounding parts by areolar tissue, which is mostly loaded with fat. In this way it is attached behind to the front of the sacrum and the coccyx, and at the sides to the coccygei and levatores ani muscles. In front, it is in immediate connection with a triangular portion of the base of the bladder (fig. 538, v'); on each side of this, with the vesiculæ seminales; and farther forwards, with the under surface of the prostate (p). Below the prostate, where the rectum turns downwards to reach the anus, it becomes invested by the fibres of the internal sphincter, and embraced by the levatores ani muscles, by which, as well as by the triangular ligament of the urethra, it is supported. Lastly, at its termination it is surrounded by the external sphincter ani muscle.

In the female, the lower portion of the rectum is firmly connected with the back of the vagina.

For convenience of description the rectum is sometimes divided arbitrarily into three parts; the first or uppermost, about 3½ inches long, extending to the centre of the 3rd sacral vertebra: the middle part (3 inches) from this point to the tip of the coccyx; whilst the lowermost, about an inch and a half long, curves backwards and downwards to the anus.

Structure of the Rectum.—The rectum differs in some respects from the rest of the large intestine, in the structure of both its muscular and its mucous coats.

The *muscular coat* is very thick: the external or longitudinal fibres form a uniform layer around it, and near the lower end of the intestine, pass between the external and internal sphincters, and end partly amongst the fibres of these muscles, partly in the skin of the anus. The internal or circular fibres become more numerous towards the anus, where they form the internal sphincter muscle. The longitudinal fibres are paler than the circular, but both layers become darker and redder towards the termination of the bowel. A pair of small bands of plain muscular tissue, which arise from the front of the second and third coccygeal vertebræ, and are also connected with the pelvic fascia, pass with a slight downward inclination to the rectum, and become intermingled with its longitudinal fibres. They are known as the recto-coccygeal muscles.

The *mucous membrane* of the rectum is thicker, redder, and more vascular than that of the colon; and it moves more freely upon the muscular coat. It presents numerous folds of different sizes, and running in various directions, nearly all of which are effaced by distension of the bowel. Near the anus these folds are principally longitudinal, and seem to depend on the contraction of the sphincter muscles outside the loosely connected mucous membrane. The larger of these

folds were named by Morgagni the *columns* of the rectum. These columns contain longitudinal muscular fibres (apparently part of the muscularis mucosæ), which terminate both superiorly and inferiorly in elastic tissue (Treitz). Higher up in the intestine, the chief folds are transverse or oblique. Three prominent folds, larger than the rest, being half an inch or more in depth, and having an oblique direction in the interior of the rectum, have been pointed out specially by Houston. One of these projects backwards from the upper and fore part of the rectum, opposite the prostate gland; another is placed higher up, at the side of the bowel; and the third still higher. From the position and projection of these folds, they may more or less impede the introduction of instruments (Dublin Hospital Reports, vol. v.). Hermann and Desfosses describe convoluted glandular tubes lying between the muscular bundles of the internal sphincter and opening on to the surface of the mucous membrane close to the anus (Compt. rend., xc. 1880).

Vessels and Nerves of the Rectum.—The *arteries* of the rectum spring from three sources, viz., the superior hæmorrhoidal branches from the inferior mesenteric; the middle hæmorrhoidal branches from the internal iliac directly or indirectly; and, lastly, the external or inferior hæmorrhoidal branch from the pudic artery. The arrangement of the vessels is not the same throughout the rectum. Over the greater part the arteries penetrate the muscular coat at short intervals, supplying its layers as they pass through, and, at once dividing into small branches in the submucosa, form a network by their intercommunication. Towards the lower end, for four or five inches, the arrangement is different. Here the vessels, having penetrated the muscular coat at different heights, assume a longitudinal direction, passing in parallel lines towards the end of the bowel. In their progress downwards they communicate with one another at intervals, and they are very freely connected near the orifice, where all the arteries join by transverse branches of considerable size (R. Quain).

The *veins* are very numerous, and form a complex interlacement resembling that of the arteries just described, and named the *hæmorrhoidal plexus*. After following a longitudinal course upwards similar to that of the arteries which they accompany, they end partly in the internal iliac vein by branches which accompany the middle hæmorrhoidal artery, and partly in the inferior mesenteric vein. Hence, the blood from the rectum is returned in part into the vena cava, and in part into the portal system.

The *lymphatics* enter some glands placed in the hollow of the sacrum, or those of the lumbar series.

The *nerves* are very numerous, and are derived from both the cerebro-spinal and the sympathetic systems. The former consist of branches derived from the sacral plexus; and the latter of offsets from the inferior mesenteric and hypogastric plexuses.

THE ANUS AND ITS MUSCLES.

The *anus*, or lower opening of the alimentary canal, is a dilatable orifice, at which the mucous membrane and skin become continuous with each other. The skin around the borders of the anus, which is thrown into wrinkles during the closed state of the orifice, is covered with numerous papillæ, and is provided with hairs and large sebaceous follicles.

The lower end of the rectum and the margin of the anus are, moreover, embraced by certain muscles, which serve to support the bowel, and to close its anal orifice. These muscles, proceeding from within outwards, are, the internal sphincter, the levatores ani, the coccygei, and the external sphincter. The three last muscles have already been described in Vol. I.

The **internal sphincter muscle** is a muscular ring or rather belt, surrounding the lower part of the rectum, an inch above the anus, and extending over about half an inch of the intestine. It is two lines thick, and is paler than the external sphincter. Its fibres are continuous

above with the circular muscular fibres of the rectum, and, indeed, it consists merely of those fibres more numerously developed than elsewhere, and prolonged farther down than the external longitudinal fibres.

Kohlrausch describes a thin stratum of fibres between the mucous membrane and the internal sphincter, these fibres having a longitudinal direction. According to Henle this is nothing more than the longitudinal fibres of the muscularis mucosæ; but Kohlrausch gives it a distinct name, the sustentator tunicæ mucosæ (corrugator cutis ani of Ellis). (Kohlrausch, Anat. und Phys. d. Beckenorgane. Leipzig, 1854; Ellis, Illustrations of Dissections, London, 1865; *Roux* in Arch. f. mikr. Anat., XIX. 1881; *Robin et Cadiat* in Journ. de l'anat., 1874.)

THE LIVER.

The **liver** is the largest gland in the body, and by far the most bulky of the abdominal viscera. It measures about 10 or 12 inches transversely from right to left, between 6 and 7 inches from its posterior to its anterior border, and about 3½ inches from above downwards where thickest, which is towards the right and posterior part. The ordinary bulk is 90 to 100 cubic inches. The ordinary weight is between 50 and 60 ounces.

The liver is solid to the feel, and of a dull reddish-brown colour, with frequently a dark-purplish tinge along the anterior margin.

According to the facts recorded by Reid, the liver weighed, in 43 cases out of 82, between 48 and 58 ounces in the adult male; and in 17 cases out of 36, between 40 and 50 ounces in the adult female. It is generally estimated to be equal to about 1-36th of the weight of the whole body; but in the fœtus, and in early life, its proportionate weight is greater.

The specific gravity of the liver is between 1·05 and 1·06: in fatty degeneration this is reduced to 1·03, or even less.

The liver is divided into two unequal lobes, a right and a left, and on the under and posterior surfaces of the right lobe are three secondary lobes or lobules, named the lobe of Spigelius, the caudate or tailed lobe, and the square lobe.

The **right** and **left lobes** are separated from each other on the under surface by the umbilical fissure (fig. 539 *u.f.*), and on the posterior surface by its prolongation the fissure for the ductus venosus (*f.d.v.*). In front, their partial limit is the interlobar notch, but on the convex surface of the liver there is no other indication of a separation between them than the line of attachment of the fold of peritoneum termed the broad ligament. The right lobe is much larger and thicker than the left, which is very variable in extent and ordinarily constitutes only about one-fifth or one-sixth of the entire gland.

The liver is usually described as having an upper convex and an under concave surface which join another at the circumference of the organ; the latter being described as thick and rounded behind and on the right, but sharp and thin in front and on the left. This description applies however, only to the organ as it is usually examined, viz.: in the soft condition, and after removal from the body. But it has been shown by His that if the organ be carefully hardened *in situ*, a considerable part of its surface (comprehending not only what was previously described as the posterior border, but also portions of what have hitherto been reckoned as belonging to the under surface, viz. a part of the left lobe, and the whole of the Spigelian lobe), looks altogether backwards, and may therefore

be more correctly described as forming a third or posterior surface. This mode of description of the surfaces will therefore be followed here.

The **upper surface** of the organ is convex, smooth, and covered with peritoneum. It is marked off into a right portion, large and convex, and a left portion, smaller and flatter, by the line of attachment of the broad ligament. It is exactly moulded to the under surface of the diaphragm, and in specimens hardened *in situ* exhibits on the left portion a shallow impression corresponding to the situation of the heart.

The **under surface** is concave and uneven. It is invested with peritoneum everywhere except where the gall-bladder (*g.bl.*) is adherent to it, and at the portal fissure (*p*) where the fold of peritoneum termed the

Fig. 539.

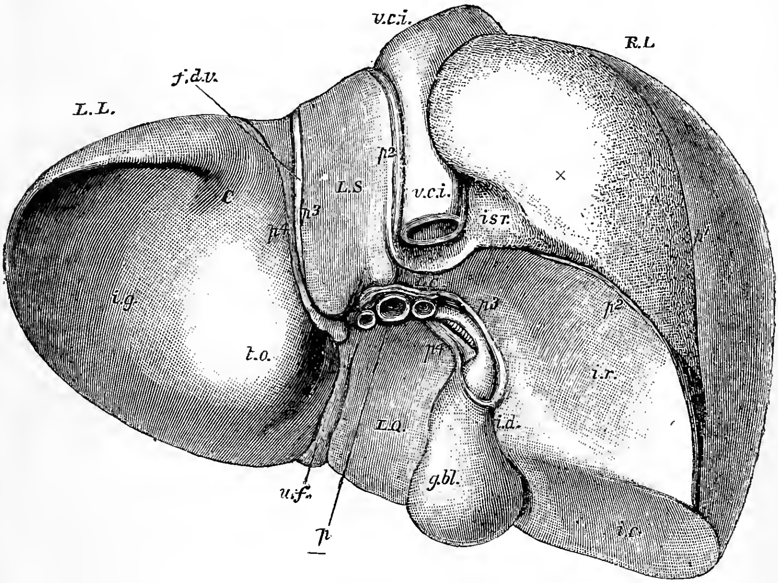


Fig. 539.—The liver of a young subject, sketched from below and behind. (The drawing has been made by Mr. Wesley from a cast prepared under the direction of Prof. His of Leipzig.) ½

R.L., right lobe; L.L., left lobe; L.S., lobe of Spigelius; L.C., caudate lobe; L.Q., quadrate lobe; *p*, portal fissure; *u.f.*, umbilical fissure; *f.d.v.*, fissure of the ductus venosus; *g.bl.*, gall-bladder; *v.c.i.*, vena cava inferior; *i.g.*, impression on the under surface of the left lobe corresponding to the stomach; *c*, position of the cardia; *t.o.*, projection of the posterior surface of the left lobe against the lesser omentum (tuber omentale, His); *i.c.*, impressio colica; *i.r.*, impressio renalis; *i.sr.*, impressio supra-renalis; p^1, p^2, p^3, p^4, lines of reflection of the peritoneum; ×, surface of the liver uncovered by peritoneum.

lesser omentum comes off, which encloses the blood-vessels and ducts of the viscus, and passes to the smaller curvature of the stomach. The under surface of the left lobe (*i.g.*) is moulded over the subjacent cardiac part of the stomach, and over that part of the anterior surface of the stomach which is next to the lesser curvature. Its free margin is sharp,

curving round and subsiding posteriorly and mesially. The surface is limited in its anterior part by the umbilical fissure, but in its posterior part it slopes gradually into the portion of the lobe which appears on the posterior surface.

The under surface of the right lobe may be regarded as divided by the fossa which lodges the gall-bladder (*fossa seu impressio vesicalis*) into two unequal portions. Of these the lateral is by far the larger, and is mainly occupied by two large shallow concave impressions, one situated anteriorly being produced by the hepatic flexure of the colon (*impressio colica, i. c.*), the other and posterior one being caused by the right kidney (*impressio renalis, i. r.*) These two impressions are separated from one another by a low ridge. At the mesial border of the renal impression is a third narrow and but slightly marked impression corresponding to the descending part of the duodenum (*impressio duodenalis, i. d.*)

The mesial of the two parts into which the fossa of the gall-bladder subdivides the under surface of the right lobe is somewhat oblong and quadrangular in shape, and is known as the *quadrate lobe* (L. Q.). It is immediately over the pyloric end of the stomach and the commencement of the duodenum, and when these are distended they impress upon the surface of the quadrate lobe a slight concavity. It is bounded on the left by the umbilical fissure and behind by the transverse or portal fissure.

The **posterior surface** of the liver, which is deeply concave opposite the convexity of the vertebral column, comprehends :—1. a portion of the left lobe which lies immediately in front of the cardia, and abuts against the anterior wall of the omental sac. That part (*c*) which is in contact with the cardia is concave, but the remainder forms a considerable protuberance (*t. o.*) projecting over the lesser curvature of the stomach. This posterior surface of the left lobe passes with a gradual slope into the under surface. 2. The *Spigelian lobe* (*lobulus Spigelii*, L. S.) and the *caudate lobe* (L. C.). The latter is a narrow ridge prolonging the Spigelian lobe towards the under surface of the right lobe. It runs behind the portal fissure, and lies immediately over the foramen of Winslow. The Spigelian lobe is separated from the left lobe by the fissure of the ductus venosus, and from the posterior surface of the right lobe by the fossa for the vena cava. Its free surface looks directly backwards, and is nearly vertical and slightly concave from side to side. Superiorly it slopes over towards the upper surface of the organ, whilst inferiorly a part of the lobe overhangs part of the transverse fissure and projects against the posterior wall of the omental sac. The Spigelian lobe is opposite the tenth and eleventh dorsal vertebræ. It rests against the crura of the diaphragm, especially the right crus, and behind the upper left hand corner the lower end of the œsophagus passes obliquely into the cardia. Lower down behind the left border is the end of the thoracic aorta separated however from the liver by the diaphragm. (3). A strip of the right lobe $2\frac{1}{2}$ to 3 inches broad ; convex for the most part except for a small depression at its lower and mesial corner which receives the right supra-renal capsule (*impressio supra-renalis, i.sr.*) In consequence of the separation of the layers of the coronary ligament this surface of the right lobe (fig. 539, ×) is not covered by peritoneum except at its right extremity. It rests against the ascending part of the diaphragm, and superiorly passes gradually into the upper surface. Inferiorly it is separated by a sharp margin from the renal impression on

the under surface. This margin is sloped obliquely downwards and outwards following the line of the 11th or 12th rib. The mesial border often projects over the vena cava.

The *transverse* or *portal fissure* (fig. 539, *p.*) is the most important, because it is here that the great vessels and nerves enter, and the hepatic duct passes out. It lies transversely between the quadrate and Spigelian lobes, and meets the longitudinal fissure nearly at right angles.

The *longitudinal fissure*, between the right and the left lobes, is divided into two parts by its junction with the transverse fissure. The anterior part (*u. f.*), named the *umbilical fissure*, contains the umbilical vein in the fœtus, and the remnant of that vein in the adult, which then constitutes the round ligament. It lies between the square and the left lobe of the liver, the substance of which often forms a bridge (*pons hepatis*) across the fissure, so as to convert it partially or completely into a canal. The posterior part (*f. d. v.*) is named the *fissure of the ductus venosus*; it is situated between the lobe of Spigelius and the left lobe, and lodges the ductus venosus in the fœtus, and in the adult a slender cord or ligament into which that vein is converted.

The *fissure* or *fossa of the vena cava* (*v. c. i.*) is situated at the back of the liver, between the Spigelian lobe and the right lobe, and is separated from the transverse fissure by the caudate lobe. It is at the bottom of this fossa that the blood leaves the liver by the hepatic veins, which end here in the vena cava. As in the case of the umbilical fissure, the substance of the liver in some cases unites around the vena cava, and encloses that vessel in a canal.

The transverse and umbilical fissures are on the under surface of the liver; the fissure of the ductus venosus and that for the vena cava are on the posterior surface.

Ligaments.—The ligaments of the liver are, with one exception, only reflections of serous membrane. Thus the name *coronary ligament* is given to the reflection of peritoneum around the somewhat triangular portion of the posterior surface of the liver (fig. 539, ×), which is here immediately adherent to the diaphragm. These reflections are continued at either end into a short fold—the *right and left lateral ligaments*, of which the left is the longer and more distinct, the right being sometimes scarcely perceptible (Struthers). Another of these so-called ligaments is the *broad, falciform*, or *suspensory ligament*, a wide thin membrane, formed of two conering layers of peritoneum continuous behind with the corresponding layers of the coronary ligaments. By one of its margins it is connected with the under surface of the diaphragm, and with the sheath of the right rectus muscle of the abdomen as low as the umbilicus; by another it is attached along the convex surface of the liver, from the posterior border to the notch in the anterior border: the remaining margin is free, and contains between its layers the *round ligament*, a dense fibrous cord, the remnant of the umbilical vein of the fœtus, which ascends from the umbilicus within the lower edge of the broad ligament, and enters the longitudinal fissure on the under surface.

Position with regard to the abdominal and thoracic parietes.—Occupying the right hypochondriac region, and extending obliquely upwards across the epigastric region into a part of the left hypochondrium, the liver is accurately adapted to the vault of the diaphragm above, and is covered, to a small extent in front, in the subcostal

angle, by the abdominal wall. At least an inch of the left lobe is to the right of the middle line. The right lobe reaches higher beneath the ribs than the left, corresponding thus with the elevated position of the diaphragm on the right side. The liver is separated by the diaphragm from the concave base of the right lung, the thin margin of which descends so as to intervene between the surface of the body, and the solid mass of the liver.

The convex surface is protected, on the right, by the 7th to the 11th ribs, and in front by the cartilages of the 6th, 7th, 8th, and 9th ribs, and by the ensiform process—the diaphragm, of course, being interposed. The situation of the liver is modified by the position of the body, and also by the movements of respiration; thus, in the upright or sitting posture, it descends to just below the lateral margin of the thorax; but in the recumbent position ascends an inch or an inch and a half higher up, and is entirely covered by the ribs, except a small portion opposite the subcostal angle. During a deep inspiration, the liver also descends below the ribs even in the recumbent posture, and in expiration, retires upwards behind them. In females it is often permanently forced downwards below the costal cartilages, owing to the use of tight stays; sometimes it reaches nearly as low as the crest of the ilium; and, in many such cases, its convex surface is indented from the pressure of the ribs.

Vessels and Nerves.—The two vessels by which the liver is supplied with blood are the hepatic artery and the portal vein. The **hepatic**

Fig. 540.

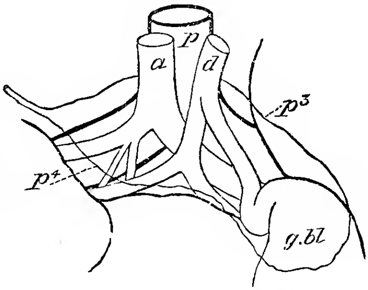


Fig. 540.—Sketch of a portion of the under surface of the liver, showing the arrangement of the vessels in the portal fissure. (G. D. Thane).

a, hepatic artery; *p*, portal vein; *d*, bile duct; *g.bl.*, gall-bladder; p^3, p^4, as in fig. 539.

artery (fig. 540, *a*), a branch of the cœliac axis, is small in comparison with the organ to which it is distributed. It enters the transverse fissure, and there divides into a right and left branch, for the two principal lobes.

By far the greater part of the blood which passes through the liver,—and in this respect it differs from all other organs of the human body,—is conveyed to it by a large vein, the **portal vein** or **vena portæ** (fig. 540, *p*). This vein is formed by the union of the veins of the stomach, intestines, pancreas and spleen. It enters the transverse fissure, or *porta hepatis*, and, like the hepatic artery, there divides into two principal branches.

The hepatic artery and portal vein, lying in company with the bile-duct, ascend to the liver between the layers of the gastro-hepatic omentum, in front of the foramen of Winslow, and thus reach the transverse fissure. In this course the bile-duct is to the right, the hepatic artery to the left, and the large portal vein behind the other two. They are accompanied by numerous lymphatic vessels and nerves. The branches of the three vessels accompany one another in their course through the liver nearly to their termination; and are surrounded for some distance by an areolar investment, the so-called capsule of Glisson, which is prolonged into the interior of the organ.

The **hepatic veins**, which convey the blood away from the liver, pursue through its substance an entirely different course from the other vessels, and pass out at its posterior border, where, at the bottom of the fossa already described, they end by two or three principal branches, besides a number of smaller ones, in the vena cava inferior.

The **lymphatics** of the liver, large and numerous, form a deep and a superficial set. Their mode of origin and their course will be afterwards described.

The **nerves** are derived partly from the cœliac plexus, and partly from the pneumogastric nerves, especially from the left pneumogastric. They enter the liver supported by the hepatic artery and its branches; along with which they may be traced a considerable way in the portal canals, but the manner of their ultimate distribution is not known.

EXCRETORY APPARATUS.—The excretory apparatus of the liver consists of the hepatic duct, the cystic duct, the gall-bladder, and the common bile-duct.

The **hepatic** duct, formed by the union of a right and left branch, which issue from the bottom of the transverse fissure and unite at a very obtuse angle, descends to the right, within the gastro-hepatic omentum, in front of the vena portæ, and with the hepatic artery to its left. Its diameter is about two lines, and its length nearly two inches. At its lower end it meets with the cystic duct, descending from the gall-bladder; and the two ducts uniting together at an acute angle, form the common bile-duct.

The **gall-bladder** (fig. 5~~4~~9, *g. bl*), is a pear-shaped membranous sac, 5/
3 or 4 inches long, about an inch and a half across its widest part, and capable of containing from 8 to 12 fluid-drachms. It is lodged obliquely in the fossa before mentioned on the under surface of the right lobe, with its large end or *fundus*, which projects beyond the anterior border of the liver, directed forwards, downwards, and to the right, whilst its *neck* is inclined in the opposite direction. Its upper surface is attached to the liver by areolar tissue. Its under surface and fundus are covered by the peritoneum, which is reflected over them from the surface of the liver. In rare cases the peritoneum completely surrounds the gall-bladder, which is then suspended by a sort of mesentery from the under surface of the liver. The fundus touches the abdominal parietes immediately beneath the margin of the thorax, opposite the tip of the tenth costal cartilage. The gall-bladder rests below on the commencement of the transverse colon; and, farther back, it is in contact with the duodenum, and sometimes with the pyloric extremity of the stomach. The *neck*, gradually narrowing, is curved like the letter S, and then, becoming much constricted, and changing its general direction altogether, it bends downwards and terminates in the cystic duct.

The gall-bladder is supplied with blood by the cystic artery, a branch of the right division of the hepatic artery, along which vessel it also receives nerves from the cœliac plexus. The cystic veins empty themselves into the vena portæ.

The **cystic duct** is about an inch and a half in length. It runs backwards, downwards, and to the left, and unites with the hepatic duct to form the common bile-duct.

The **common bile-duct**, *ductus communis choledochus*, from two to three lines in width, and nearly three inches in length, conveys the bile into the duodenum. It passes downwards and backwards, continuing the course of the hepatic duct, between the layers of the gastro-hepatic omentum, in front of the vena portæ, and to the right of the hepatic artery. Passing behind the first part of the duodenum it reaches the descending portion and continues downwards on the inner and posterior aspect of that part of the intestine, covered by or included in the head of the pancreas, and for a short distance in contact with the right side of the pancreatic duct. Together with that duct, it then perforates the muscular wall of the duodenum, and, after running obliquely for three quarters of an inch between its coats, and forming an elevation beneath the mucous membrane, it becomes somewhat constricted, and opens by a common orifice with the pancreatic duct on the inner surface of the intestine, near the junction of the second and third portions of the duodenum, and three or four inches beyond the pylorus, as already described.

Varieties.—The liver is not subject to great or frequent deviation from its ordinary form and relations. Sometimes it retains the thick rounded form which it presents in the fœtus; and it has occasionally been found without any division into lobes. On the other hand, Sœmmerring has recorded a case in which the adult liver was divided into twelve lobes; and similar cases of subdivided liver (resembling that of some animals) have been now and then observed by others. A detached portion, forming a sort of *accessory* liver, is occasionally found appended to the left extremity of the gland by a fold of peritoneum containing blood-vessels.

The gall-bladder is occasionally wanting, in which case the hepatic duct is much dilated within the liver, or in some part of its course. Sometimes the gall-bladder is irregular in form, or is constricted across its middle, or, but much more rarely, it is partially divided in a longitudinal direction. Direct communications by means of small ducts (named hepato-cystic), passing from the liver to the gall-bladder, exist regularly in various animals; and they are sometimes found, as an unusual formation, in the human subject.

The right and left divisions of the hepatic duct sometimes continue separate for some distance within the gastro-hepatic omentum. Lastly the common bile-duct not unfrequently opens separately from the pancreatic duct, into the duodenum.

STRUCTURE OF THE LIVER.

The liver has two coverings, viz., a serous or peritoneal, already sufficiently referred to, and a proper areolar coat.

The *areolar* or *fibrous* coat invests the whole gland. Opposite to the parts covered by the serous coat, it is thin and difficult to demonstrate; but where the peritoneal coat is absent, as at the posterior border of the liver, and in the portal fissure, it is denser and more evident. Its inner surface is attached to the hepatic glandular substance, being there continuous with the delicate areolar tissue which lies between the small lobules of the gland. At the transverse fissure it becomes continuous with the *capsule of Glisson*, by which name, as already noticed, is

designated a strong sheath of areolar tissue which surrounds the branches of the portal vein, hepatic artery, and hepatic duct, as they ramify in the substance of the liver, but which becomes more delicate as it passes on to the smaller vascular branches.

Hepatic lobules.—The proper substance of the liver, which has a mottled aspect when closely observed, is compact, but not very firm. It is easily cut or lacerated, and is not unfrequently ruptured during life from accidents in which other parts of the body have escaped injury. When the substance of the liver is torn, the broken surface is not smooth, but coarsely granular, the liver being composed of a multitude of small lobules (fig. 541), which vary from $\frac{1}{24}$th to $\frac{1}{12}$th of an inch in diameter (1—2 millimetres).

Fig. 541.

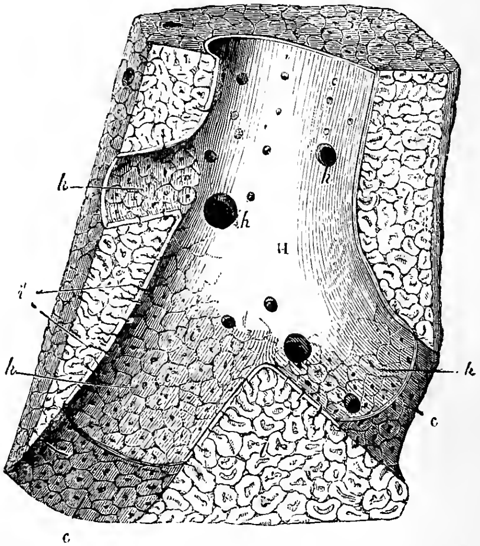


Fig. 541.—Section of a portion of liver passing longitudinally through a considerable hepatic vein, from the pig (after Kiernan). About 5 Diameters.

H, hepatic venous trunk, against which the sides of the lobules are applied; *h*, *h*, *h*, three sublobular hepatic veins, on which the bases of the lobules rest, and through the coats of which they are seen as polygonal figures; *i*, mouth of the intralobular veins, opening into the sublobular veins; *i'*, intralobular veins shown passing up the centre of some divided lobules; *c*, *c*, walls of the hepatic venous canal, with the polygonal bases of the lobules.

These lobules in some animals, as in the pig and camel, are completely isolated one from another by areolar tissue continuous with the fibrous coat of the liver, and with the capsule of Glisson; but in the human subject, and in most animals, although very distinguishable, they are not completely insulated, being confluent in a part of their extent.

The lobules of the liver have, throughout its substance, in general the polyhedral form of irregularly compressed spheroids; but on the surface they are flattened and angular. They are all compactly arranged around the sides of branches (*sublobular*) of the hepatic veins (fig. 541), each lobule resting by a smooth surface or *base*, upon the vein, and being connected with it by a small venous trunklet (*intralobular*), which begins in the centre of the lobule, and passes out from the middle of its base, to end in the larger subjacent vessel. If one of the sublobular veins be opened (as in the figure), the bases of the lobules may be seen through the coats of the vein, which are here very thin, presenting a tesselated appearance, each little polygonal space representing the base of a lobule, and having in its centre a small spot, which is the mouth of the intralobular vein (*i*).

Each lobule consists of a mass of cells penetrated from the circumference to the centre by a close network of blood-capillaries, as well

Fig. 542.

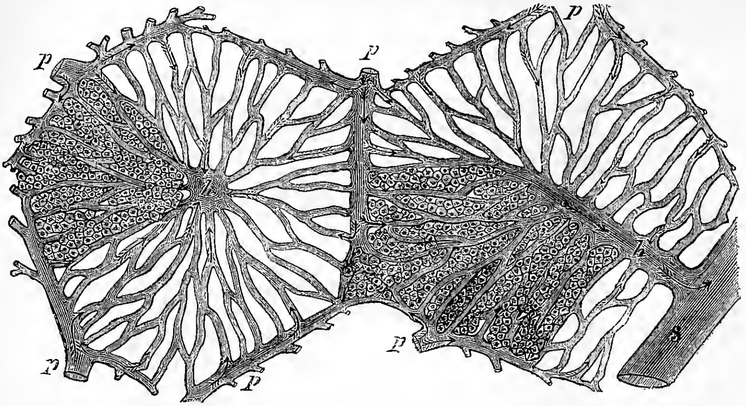


Fig. 542.—Diagrammatic representation of two hepatic lobules (E.A.S.)

The left-hand lobule is represented with the intralobular vein cut across; in the right-hand one the section takes the course of the intralobular vein. P, interlobular branches of the portal vein; H, intralobular branches of the hepatic veins; S, sublobular vein; C, capillaries of the lobules. The arrows indicate the direction of the course of the blood. The liver-cells are only represented in one part of each lobule.

as by the minute capillary commencements of the bile-ducts, with the intervention of little other tissue. For the sake of clearness, the disposition of the vessels of the liver may be considered first.

Blood-vessels.—The portal vein and hepatic artery, accompanied by

Fig. 543.

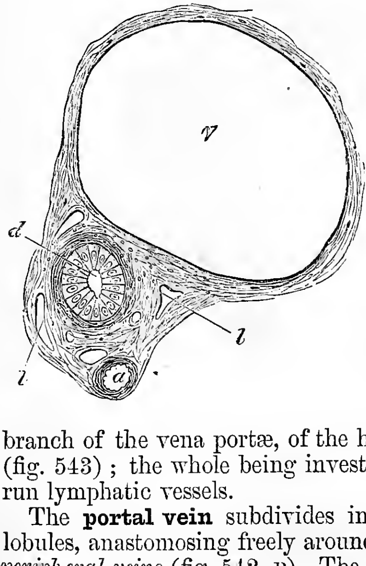


Fig. 543.—Section of a portal canal (E.A.S.).

a, branch of hepatic artery; *v*, branch of portal vein; *d*, bile-duct; *ll*, lymphatics in the areolar tissue of Glisson's capsule which encloses the vessels.

the emerging biliary ducts, enter the liver at the transverse fissure. Within the liver the branches of these three vessels lie together in certain canals, called *portal canals*, which are tubular passages formed in the substance of the gland, commencing at the transverse fissure, and branching upwards and outwards from that part in all directions. Each portal canal (even the smallest) contains one principal branch of the vena portæ, of the hepatic artery, and of the biliary duct (fig. 543); the whole being invested by connective tissue, within which run lymphatic vessels.

The **portal vein** subdivides into branches which ramify *between* the lobules, anastomosing freely around them, and are named *interlobular* or *peripheral veins* (fig. 542, P). The branches of these pass into the lobules

at their circumference and end in the capillary network, from which the intralobular or central veins take origin. Within the portal canals the branches of the portal veins receive small veins which are returning blood distributed by branches of the hepatic artery.

Fig. 544.

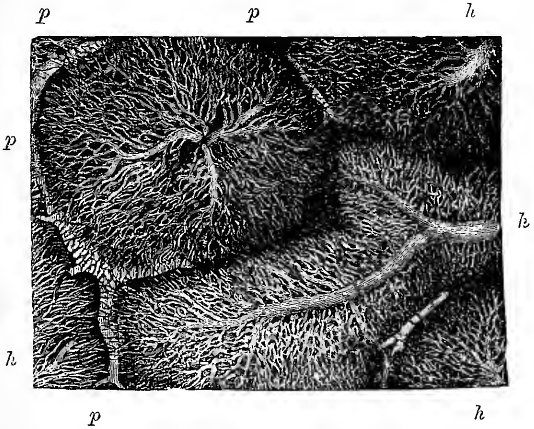


Fig. 544.—Capillary network of the lobules of the rabbit's liver (from Kölliker). About 40 diameters.

The figure is taken from a very successful injection of the hepatic veins made by Harting: it shows nearly the whole of two lobules, and parts of three others: *p*, portal branches running in the interlobular spaces; *h*, hepatic veins radiating from the centre of the lobules.

Fig. 545.

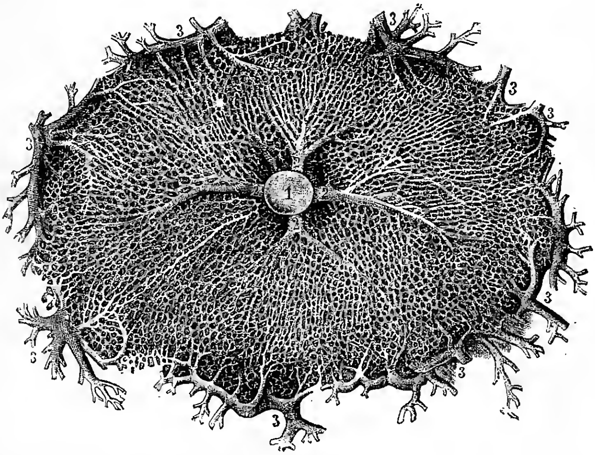


Fig. 545.—Cross section of a lobule of the human liver, in which the capillary network between the portal and hepatic veins has been fully injected (from Sappey). 60 diameters.

1, section of the intralobular or central vein; 2, its smaller branches collecting blood from the capillary network; 3, interlobular or peripheric branches of the vena portæ with their smaller ramifications passing inwards towards the capillary network in the substance of the lobule.

The **hepatic artery** terminates in three sets of branches, termed vaginal, capsular, and interlobular. The *vaginal* branches ramify within the portal canals, supplying the walls of the ducts and vessels, and the accompanying connective tissue. The *capsular* branches appear on the surface of the liver spread out on the fibrous coat, accompanied by their veins. The *interlobular* branches accompany the interlobular veins, but are much smaller; they supply blood to the walls of these and the accompanying bile-ducts; it is doubtful if they transmit any blood directly to the capillary network of the lobules.

The **capillary network** of the lobules is very close, so that commonly the interval between two vessels is not greater than the diameter of one or two liver cells (fig. 542). Moreover the vessels are comparatively large ($\frac{1}{2500}$th of an inch), and in specimens in which they have been filled with transparent injection, can be seen, not only to pass in a radiating manner, as before described, between the intra- and inter-lobular veins, but also in the human subject to be continued from one lobule to another.

Fig. 546.

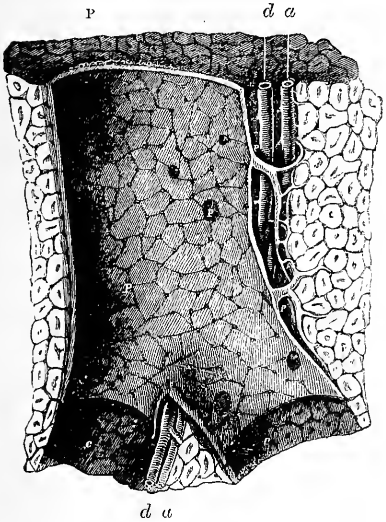


Fig. 546.—Longitudinal section of a portal canal, containing a portal vein, hepatic artery, and hepatic duct, from the pig (after Kiernan). About 5 diameters.

P, branch of vena portæ, situated in a portal canal, formed amongst the hepatic lobules of the liver; *p*, *p*, larger branches of portal vein, giving off smaller ones named interlobular veins; there are also seen within the large portal vein numerous orifices of interlobular veins arising directly from it; *a*, hepatic artery; *d*, biliary duct; at *c*, *c*, the venous wall has been partially removed.

The capillaries are accompanied by a very small amount of connective tissue, containing flattened and stellate cells. This tissue occurs more abundantly near the centre of the lobule around the intralobular vein; and both here and in that accompanying the interlobular veins, there are numerous granular connective tissue cells.

The **hepatic veins** commence in the centre of each lobule by the convergence of its capillaries into the single independent *intralobular* or *central vein* (figs. 542, H; 544, *h*; and 545, 1), as already stated. These minute intralobular veins open at once into the sides of the adjacent *sublobular* veins (fig. 542, S), which are of various sizes, and join to form larger and larger vessels, ending at length in hepatic venous trunks, which receive no intralobular veins. Lastly, these venous trunks, converging towards the posterior border of the liver, and receiving in their course other sublobular veins, terminate in the vena cava inferior, as already described. In this course the hepatic veins and their successive ramifications are unaccompanied by any but lymphatic vessels. Their coats are thin; the sublobular branches adhere closely to the lobules, and even the larger trunks have but a slight areolar investment connecting

them to the substance of the liver. Hence the divided ends of these veins are seen upon a section of the liver as simple open orifices, the thin wall of the vein being surrounded closely by the solid substance of the gland.

The hepatic cells.—The interstices between the blood-vessels are, as before said, almost entirely filled by the hepatic cells. These are of a compressed spheroidal or polyhedral form, having a mean diameter of from $\frac{1}{1080}$th to $\frac{1}{840}$th of an inch. They possess no cell membrane. Their substance appears granular and of a faint yellowish tinge, and they contain each a clear round nucleus, with intra-nuclear network and one or

Fig. 547.

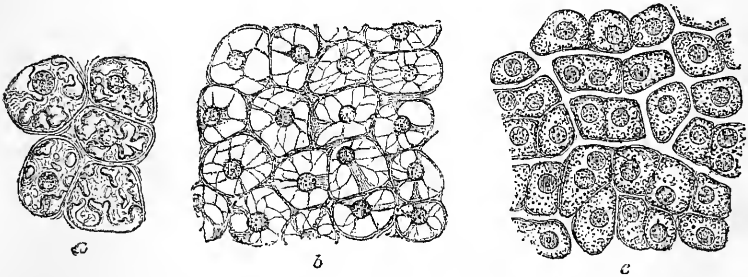


Fig. 547.—Hepatic cells from the liver of a dog (Heidenhain), 14 hours after a full meal.

a, with glycogenic deposit; *b* and *c*, after its solution. In *c* the network of protoplasm which remains is finer than in *b*, and imparts a somewhat granular appearance to the cells. The external layer of the protoplasm contains no glycogen.

two nucleoli. Not unfrequently two nuclei are to be found in a cell. In many cases especially with a fatty diet, the cells are found to have large or small fat-globules in their interior; this fatty deposit is much more abundant in the cells which are near the periphery than in those near the centre of the lobule. When isolated in the fresh condition they are said to exhibit slow changes of form. The liver-cells are packed between and around the vessels, and in sections made at right angles to the intralobular veins, appear as if radiating from the centre of the lobules towards their circumference. They form a continuous network, or spongework, the more obvious openings in which are the spaces occupied by the blood-capillaries. The walls of the latter are not everywhere in contact with the liver cells, but are separated from them in parts by a cleft-like lymphatic space which is only imperfectly marked off by the flattened and stellate connective tissue cells before mentioned (p. 246).

The hepatic cells frequently contain glycogen especially after a heavy meal of starchy matters. It occurs in globules or in irregular amorphous masses within them (Heidenhain), and when abundant reduces the protoplasm of the cell to the condition of an open network, which becomes very distinct after solution of the glycogen (fig. 547). When these masses of glycogen are not present the protoplasm exhibits after hardening a finely reticulated appearance (Klein, Langley). (See fig. 45.)

Commencement of the ducts.—When a thin section of the hardened tissue is examined under a high power of the microscope, minute apertures

may occasionally be observed between the opposed sides of adjacent liver-cells. These are the sections of fine intercellular passages (*bile-canaliculi*) which form a close network (fig. 548) between and around the individual cells, much finer and closer than the blood-capillary network, from the branches of which they run apart. These passages,

Fig. 548.

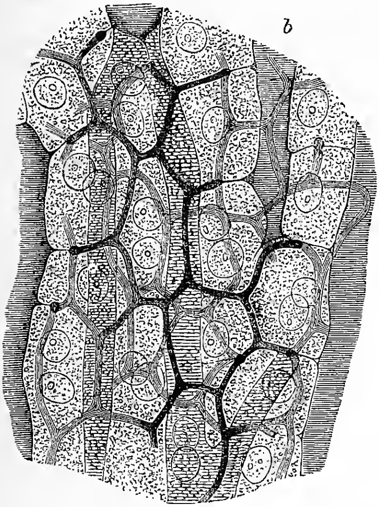


Fig. 548.—Section of rabbit's liver with the intercellular network of bile-canaliculi injected. Highly magnified (Hering).

Two or three layers of cells are represented; *b*, *b*, blood capillaries.

which are bounded by a very delicate proper wall, are the commencements of the biliary ducts, into which at the circumference of the lobule they open. They may be injected from the trunk of the bile duct, at least in the outer parts of the lobule.

To demonstrate the intercellular network throughout the whole extent of the lobules, Chrzonszczewsky employed a method of natural injection. He introduced a saturated watery solution of pure sulph-indigotate of soda, in repeated doses, into the circulation of dogs and sucking-pigs, by the jugular vein; and in an hour and a half afterwards the animals were killed and the blood-vessels either washed out with chloride of potassium introduced by the portal vein, or were injected with gelatine and carmine. In specimens prepared in this way the fine network of bile-ducts throughout each lobule is filled with blue, while the intervening cells remain free from colour. By killing the animals sooner after the injection, the blue colouring matter was found within the hepatic cells, thus demonstrating that it was through their agency that the canals were filled.

From the observations of Pflüger and of Kupffer it would appear that the relation between the hepatic cells and the bile-canaliculi is even more intimate than has been generally supposed. For both by the methods of artificial and of natural injection, they have demonstrated the existence of vacuoles within the cells communicating by exceedingly minute intracellular channels with the adjoining bile-canaliculi (see fig. 549).

In the lower vertebrates and in the earlier stages of development in birds and mammals the liver is a tubular gland, composed of anastomosing tubules, with narrow lumina (biliary canaliculi), and directly continuous with the ducts. In all animals the bile-canaliculi are separated by at least a portion of a cell from the nearest blood capillaries.

Structure of the ducts.—The minute ramifications between the lobules have walls composed of fibrillar connective tissue, within which is a basement membrane, and a lining of short columnar epithelium. According to Heidenhain they also possess both longitudinally and circularly disposed muscular cells in their wall. As they pass into the lobules, the columnar epithelium becomes shorter and flatter, the tube at the same time branching both laterally and terminally and

becoming much reduced in size so that only a very small lumen is left. The basement membrane is no longer complete, and the intercellular bile passages open directly into the minute ducts, the hepatic cells abutting against the flattened epithelium of the latter.

In the portal canals, where they are somewhat larger, the ducts present numerous openings on the inner surface, which are scattered irregularly in the larger ducts, but in the subdivisions are arranged in two longitudinal rows, one at each side of the vessel. These openings were formerly supposed to be the orifices of mucous glands; but, while the main ducts are studded with true mucous glands of lobulated form and with minute orifices, the openings now referred to belong to saccular and tubular recesses, which are often branched and anastomosing, and may be beset all over with cæcal projections (Theile). The larger bile-ducts have areolar coats, containing abundant elastic tissue, and a certain amount of plain muscular tissue disposed both longitudinally and circularly. They are lined with columnar epithelium.

Fig. 549.

A B

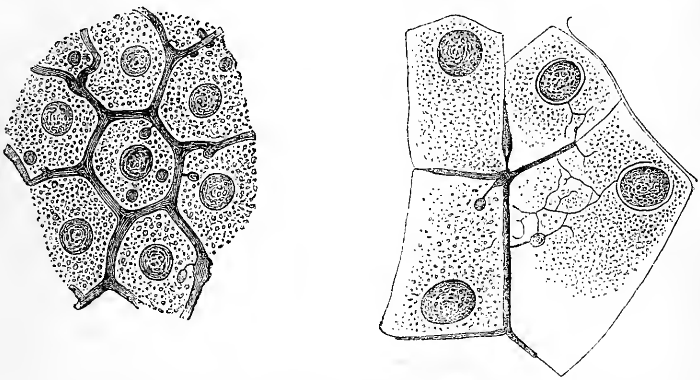


Fig. 549.—Sketches illustrating the mode of commencement of the bile-canaliculi within the liver-cells (Heidenhain after Kupffer).

A. Canaliculi of the rabbit's liver, artificially injected from the hepatic duct, with Berlin blue solution. The intercellular canaliculi are seen to give off minute twigs, which penetrate into the liver-cells, and there terminate in vacuole-like enlargements.

B. From a frog's liver naturally injected with sulph-indigotate of soda. A similar appearance is obtained, but the communicating twigs are ramified.

In the duplicature of peritoneum forming the left lateral ligament of the liver, and also in the two fibrous bands which sometimes bridge over the fossa for the vena cava and the fissure of the umbilical vein, there have been found biliary ducts of considerable size which are not surrounded with lobules. These *aberrant ducts* as they are called, were described by Ferrein and afterwards by Kiernan; they anastomose together in form of a network, and are accompanied by branches of the vena portæ, hepatic artery, and hepatic vein. They represent portions of hepatic substance which were present at an early period of development but have subsequently become atrophied.

Lymphatics of the liver.—Lymphatics are seen in the prolongations of Glisson's capsule between the lobules (*interlobular lymphatics*), where they accompany the blood-vessels, and in some cases surround and enclose them. They originate from the lymphatic spaces around the capillaries of the lobules (p. 247). They unite into larger vessels which run along the portal canals and emerge at

the portal fissure. Other lymphatic vessels accompany the branches of the *hepatic* veins, also conveying lymph from the perivascular lymphatics of the lobules. There is further a close *subperitoneal plexus* on the surface of the organ, which on the upper surface communicates, through the ligaments of the liver, with the thoracic lymphatics, and on the under surface with the lymphatics of Glisson's capsule.

In the pig's liver lymphoid follicles have been noticed by Kisselew and Chrzonszczewsky, in connection with the interlobular lymphatics.

Structure of the Gall-bladder.—Besides the peritoneal investment and the mucous lining, the gall-bladder possesses an intermediate muscular and connective tissue coat, of considerable strength. This consists mainly of bands of dense shining white fibres, which interlace in all directions. Intermingled with these are plain muscular fibres, which have principally a longitudinal direction, but some run transversely. This coat forms the framework of the organ, and supports the larger blood-vessels and lymphatics. The nerves form a gangliated plexus within it; partly also immediately beneath the serous coat (L. Gerlach).

The *mucous membrane*, which after death is generally strongly tinged with bile, is elevated upon its inner surface into very numerous small ridges, which, uniting together into meshes, leave between them depressions of different sizes and of various polygonal forms. This gives the interior of the gall-bladder an alveolar aspect, similar to what is seen on a smaller scale in the vesiculæ seminales. These alveolar intervals become smaller towards the fundus and neck of the gall-bladder; and at the bottom of the larger ones, other minute depressions, which may be seen with a simple lens, lead into numerous mucous recesses. The whole of the mucous membrane is covered by columnar epithelium, and it secretes an abundance of viscid mucus. The blood-vessels form a close network near the surface of the mucous membrane, and there is also a fine lymphatic plexus in the mucous membrane, communicating with a network of larger vessels in the serous coat.

At the places where the neck of the gall-bladder curves on itself there are strong folds of its mucous and areolar coats projecting into the interior.

In the *cystic duct*, the mucous membrane is elevated internally in a similar manner into a series of crescentic folds, which are arranged in an oblique direction, and succeed closely to each other, so as to present very much the appearance of a continuous spiral valve. When distended, the outer surface of the duct appears to be indented in the situation of these folds, and dilated or swollen in the intervals, so as to present an irregularly sacculated or twisted appearance. In the structure of its wall, the cystic duct resembles the gall-bladder.

Recent Literature.—On the structure of the liver generally: *Hering*, in Stricker's Handbook, 1871; *Heidenhain*, in Hermann's Handbuch, 1880. On the origin of the bile-ducts: *Kupffer*, in Tagebl. d. 46 Versamml. d. Naturf., 1873, and in Schriften d. naturw. Ver. f. Schleswig-Holstein, III.; *Legros*, in Journ. de l'anat., 1874; *Asp*, in Sächs. Bericht., 1873; *Peszke*, Beiträge, &c., Dorpat, 1874; *Popoff*, in Virch. Arch., LXXXI. On the terminations of the hepatic artery: *Cohnheim* u. *Litten*, in Virch. Arch., LXVII. On the connective tissue of the liver: *Fleischl*, in Sächs. Bericht., 1874; *Kupffer*, in Arch. f. mikr. Anat., XII., 1875; *Turner* (camel's liver), in Journal of Anat. and Physiol. XI., 1877. On the structure of the gall-bladder: *Deutsch*, Dissert. Berlin, 1875. On the position and form of the liver: *His*, in Arch. f. Anat. (u. Physiol.), 1878.

THE PANCREAS.

The *pancreas* (figs. 550, 551, P) is a long gland of a reddish cream colour and irregularly prismatic shape, which lies across the posterior wall of the abdomen, behind the stomach, and opposite the first lumbar vertebra. Its right end is the larger and is termed the *head* (P′): it is embraced by the curvature of the duodenum (*d*), whilst the left extremity, or *tail*, is in contact with the spleen (*spl*). It is moulded over the front of the vertebral column, but the crura of the diaphragm and the great vessels lie between it and the spine. Its head forms a considerable

downward projection following the curve of the duodenum, and from its upper border another well marked protuberance rises up to reach the lesser curvature of the stomach, and to abut against the posterior wall of the omentum opposite to the similar projection on the left lobe of the liver (see fig. 550).

The pancreas varies considerably, in different cases, in its size and weight. It is usually from 6 to 8 inches long, about $1\frac{1}{2}$ inches in average breadth, and from half an inch to an inch in thickness, being thicker at its head and along its upper border than elsewhere. The weight of the gland, according to Krause and Clendenning, is usually from $2\frac{1}{4}$ oz. to $3\frac{1}{2}$ oz.; but Meckel has noted it as high as 6 oz., and Sœmmerring as low as $1\frac{1}{2}$ oz.

Fig. 550.

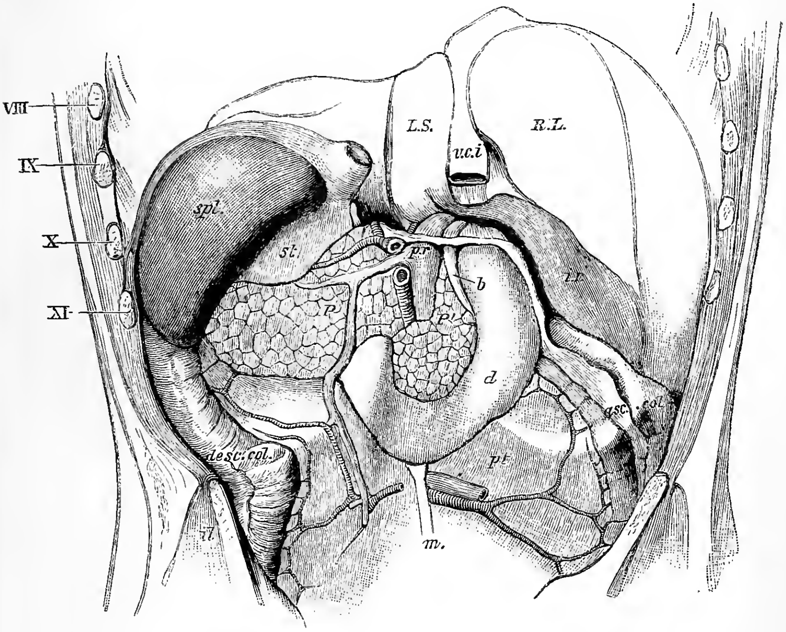


Fig. 550.—View of the abdominal viscera from behind, after removal of the spinal column and the whole of the posterior wall of the abdomen, the peritoneum being left (this and the next figure are taken from Prof. His' models). $\frac{1}{3}$

P, pancreas; *P'*, its head; *d*, duodenum; *st*, stomach; *spl*, spleen; *R.L.*, right lobe of the liver; *L.S.*, Spigelian lobe; *v.c.i.*, vena cava inferior; *p.r.*, portal vein; *b*, common bile duct; *i.r.*, impression for the right kidney on the posterior surface of the liver; the situation of the two kidneys is well shown by the corresponding impressions in the cast; *asc. col.*, *desc. col.*, ascending and descending colon; *pt*, back of the peritoneum; *m*, line of reflection of the mesentery seen through; VIII, IX, X, XI, the corresponding ribs; *il*, ilium.

The pancreas has three surfaces, viz.: anterior, posterior and a narrow inferior surface (His). These surfaces, like those of the liver, are moulded to the adjacent organs.

The *anterior surface*, somewhat concave, is covered by the stomach, which rests upon it.

The *posterior surface* is attached by areolar tissue to the vena cava,

the aorta, the superior mesenteric artery and vein, the commencement of the vena portæ, and the pillars of the diaphragm, all of which parts, besides many lymphatic vessels and glands, are interposed between it and the spine: to the left of the vertebral column it is attached similarly to the left suprarenal capsule and kidney and to the renal vessels. Of the large vessels situated behind the pancreas, the superior mesenteric artery and vein are embraced by the substance of the gland, the lower extremity of the head curving somewhat behind them,* so as sometimes to enclose these vessels in a complete canal. They pass downwards and forwards, and emerge from beneath the lower border of the pancreas, between it and the termination of the duodenum (fig. 551). The cœliac axis is above the pancreas; and in a groove along the posterior surface and upper border of the gland are placed the splenic artery and

Fig. 551.

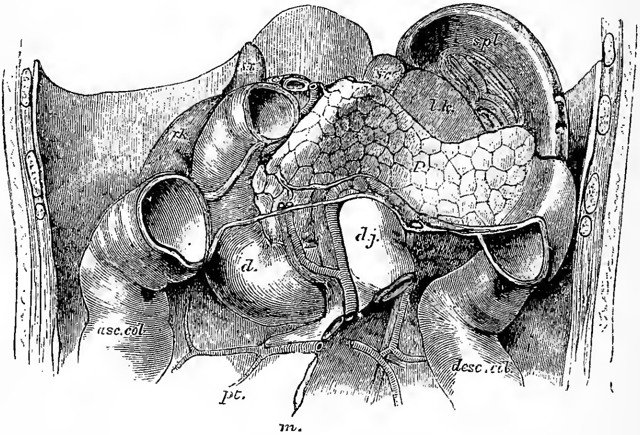


Fig. 551.—The pancreas and adjoining viscera from before. $\frac{1}{3}$.

The stomach, the greater part of the small intestines, and the transverse colon have been removed. *P*, pancreas; *d*, duodenum; *d.j*, its junction with the jejunum; above the duodenum, and between it and the head of the pancreas are seen the bile duct, portal vein, and hepatic artery; *asc. col.*, *desc. col.*, ascending and descending colon; *spl.* spleen; *r.k.*, *l.k.*, right and left kidneys; *s.r.*, *s.r′*, right and left suprarenal capsules; *pt*, peritoneum at the back of the abdominal cavity; *m*, line of reflection of the mesentery; the line of reflection of the transverse mesocolon is seen along the lower edge of the pancreas and crossing the duodenum.

vein, the vein pursuing a straight, and the artery a tortuous course, and both supplying numerous branches to the pancreas, the narrow extremity of which is attached to the inner or anterior surface of the spleen.

The common bile duct passes down behind the head of the pancreas (fig. 550, *b*), and is generally received into a groove or canal in its substance.

The *inferior surface* is very narrow. The border which separates it from the anterior surface is turned towards the root of the mesocolon, while the inferior surface itself rests at one end on the junction of duodenum and jejunum; at the other or left end on the extremity of

* This part of the gland is sometimes marked off from the rest, and is then named the *lesser pancreas.*

the transverse colon, and between these points is turned towards the general mass of the intestinal convolutions. This part of the inferior surface has a special covering of peritoneum derived from the lower layer of the mesocolon.

The principal excretory duct called the **pancreatic duct** or **canal of Wirsung**, runs through the entire length of the gland, from left to right, buried completely in its substance, and placed rather nearer its lower than its upper border. Commencing by the union of the small ducts derived from the groups of lobules composing the tail of the pancreas, and receiving in succession at various angles, and from all sides, the ducts from the body of the gland, the canal of Wirsung increases in size as it advances towards the head of the pancreas, where, amongst other large branches, it is usually joined by one derived from that portion of the gland called the lesser pancreas. Curving slightly downwards, the pancreatic duct then comes into contact with the left side of the common bile duct, which it accompanies to the posterior part of the descending portion of the duodenum. Here the two ducts, placed side by side, pass very obliquely through the muscular and areolar coats of the intestine, and terminate, as already described, on its internal surface, by a common orifice, situated at the junction of the second and third portions of the duodenum, between three and four inches below the pylorus. The pancreatic duct, with its branches, is readily distinguished within the glandular substance, by the very white appearance of its thin fibrous walls. Its widest part, near the duodenum, is from $\frac{1}{12}$th to $\frac{1}{9}$th of an inch in diameter, or nearly the size of an ordinary quill. It is lined by a remarkably thin and smooth membrane, which near the termination of the duct may present a few scattered recesses.

Varieties.—Sometimes the duct is double up to its point of entrance into the duodenum; and a still further deviation from the ordinary condition is not unfrequently observed, in which there is a *supplementary* duct, derived from the lesser pancreas or some part of the head of the gland, opening into the duodenum by a distinct orifice, at a distance of an inch or more from the termination of the principal duct. It sometimes occurs that the pancreatic duct and the common bile duct open separately into the duodenum.

Vessels and Nerves.—Like the salivary glands, the pancreas receives its blood-vessels at numerous points. Its arteries are derived from the splenic and from the superior and inferior pancreatico-duodenal branches of the hepatic and superior mesenteric. Its blood is returned by the splenic and superior mesenteric veins. Its lymphatics terminate in the lumbar vessels and glands. The nerves of the pancreas are derived from the solar plexus.

Structure.—The pancreas belongs to the class of acino-tubular glands. In its general characters it closely resembles the salivary glands, but it is somewhat looser and softer in its texture than those organs, the lobes and lobules being less compactly arranged.

The ducts are lined with a simple layer of columnar epithelium, the cells becoming shorter and more cubical in the smaller ducts. They do not exhibit any well-marked longitudinal striation like that met with in the duct-cells of some of the salivary glands. The ultimate branches of the ducts which are connected with the alveoli (intercalary ducts), are much narrowed, and are lined with flattened cells, looking spindle-shaped in optical section. The alveoli of the gland are distinctly tubular, and frequently convoluted. In the inactive condition of the gland, and during the earlier stages of activity, the alveoli are almost

completely occupied by the secreting cells, scarcely any lumen being visible. Moreover the middle of the alveolus is in many parts occupied by spindle-shaped cells (centro-acinar cells) which according to Langerhans are continuous with the epithelium-cells of the intercalary ducts.

Fig. 552.

Fig. 552.—Section of the pancreas of the dog. (Klein.)

d, termination of a duct in the tubular alveoli, *a*: the two zones in the alveolar cells are well seen.

The secreting cells of the pancreas have a very characteristic appearance. In shape they are broadly columnar, in some parts approaching the polygonal form, and they show very distinctly, even in the inactive condition of the gland, two parts or zones; an inner granular zone next the lumen, and an outer clear and finely striated zone next the basement membrane (fig. 552).

When the gland is stimulated to activity the cells at first enlarge and bulge the basement membrane; subsequently the granules of the inner zone become fewer in number and aggregated near the lumen, and the outer clear zone extends over the greater part of the cell (Heidenhain, Kühne and Lea).

Various observers after forcing injections into the alveoli of the pancreas backwards from the duct, have seen fine intercellular canaliculi, comparable to those of the liver, passing from the lumen of an alveolus between the secreting cells.

Fig. 553.

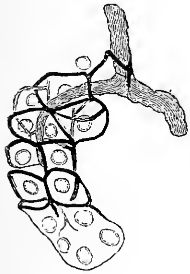


Fig. 553.—An alveolus of the pancreas injected from the excretory duct (Saviotti). Highly magnified.

The alveolar cells and nuclei are only faintly indicated; those of the duct are not represented at all. The injection is seen filling the central cavity of the alveolus, and passing from this in fine channels (represented by black reticulating lines) between and around the cells (after Saviotti).

The connective tissue of the gland, after forming a sort of external investment, penetrates between its lobes or lobules conveying the blood-vessels to all parts. They are not however everywhere equally numerous, for some acini are not surrounded by the capillary network. On the other hand in certain parts of the interalveolar tissue collections of small cells are met with which are surrounded with a very close network of large convoluted capillaries. The cells in question look like small epithelium-cells but their meaning is entirely unknown. The lymphatics of the pancreas have the same arrangement as in the salivary glands.

The mode or termination of the nerves, which are almost exclusively non-medullated, has not been ascertained.

Recent Literature.—*Langerhans*, Beiträge, &c., Berlin, 1869; Saviotti, Arch. f. mikr. Anat., V. 1869; *Latschenberger* in Wiener Sitzungsb., 65, 1872; *Heidenhain* in Pflüger's Arch., X. 1875; and Article "Absonderung," in Hermann's Handbuch, 1880; *Kühne u. Lea* in Heidelberg Verhandl. I. 1876; *G. & F. Hoggan* in Journ. of Anat., 1881 (efferent lymphatics in rodents).

THE SPLEEN.

The spleen (figs. 550, 551, *spl*) is a soft highly vascular and easily distensible organ, of a dark purplish grey colour. It is placed obliquely in the back of the left hypochondrium, between the cardiac end of the stomach, and the diaphragm, and in the line of the axilla extends from the 8th to the 11th rib. It is the largest of the organs termed ductless glands.

The shape of the spleen is variable, but when examined in the ordinary way after removal from the body, it usually appears either flattened or concavo-convex. But if previously hardened *in situ* it is found to present a somewhat compressed oval shape, having three surfaces. Of these, one, the external and posterior, is large and convex, fitting against the commencement of the arch of the diaphragm, and looking upwards, backwards, and to the left. A second, the narrowest, is placed vertically, and looks directly inwards, being applied to the outer border of the left kidney ; whilst the third surface, which is separated from that last described by a distinct vertical ridge, is larger than it, and concave. This surface is applied to the great cul-de-sac of the stomach, and is in contact also with the tail of the pancreas, and with the extremity of the arch of the colon (splenic flexure). Near the ridge above mentioned there is a vertical fissure in the anterior surface, at the part where the vessels and nerves enter the organ (see fig. 551) ; this part is termed the *hilus*. On either side of the hilus, the peritoneum, which covers the whole of the rest of the spleen, leaves the organ, and passes, as the gastro-splenic omentum, into continuity with the left border of the great omentum, attaching the spleen to the left extremity of the stomach. In some cases there is no distinct fissure at the hilus. The anterior border is often slightly notched, especially towards the lower part (fig. 551). The lower end of the organ is pointed, and rests on the costo-colic ligament.

The spleen varies in magnitude more than any other organ in the body ; and this not only in different subjects, but, as may be ascertained by percussion, in the same individual, under different conditions. On this account it is difficult or impossible to state what are its ordinary weight and dimensions : in the adult it measures generally about 5 or $5\frac{1}{2}$ inches in length, 3 or 4 inches in breadth, and 1 or $1\frac{1}{2}$ inch in thickness ; and its usual volume, according to Krause, is from $9\frac{3}{4}$ to 15 cubic inches. After the age of forty the average weight gradually diminishes. In intermittent and some other fevers the spleen is much enlarged, reaching below the ribs, and often weighing as much as 18 or 20 lbs.

Small detached roundish nodules are occasionally found in the neighbourhood of tne spleen, similar to it in substance. These are commonly named accessory or supplementary spleens (splenculi ; lienculi). One or two most commonly occur, but a greater number, and even up to twenty-three, have been met with. They are small rounded masses, varying from the size of a pea to that of a walnut. They are usually situated near the lower end of the spleen, either in the gastro-splenic omentum, or in the great omentum.

STRUCTURE OF THE SPLEEN.

The spleen has two membranous investments—a serous coat derived from the peritoneum, and a special tunic. The soft substance (pulp) of the organ is supported by a reticular framework of whitish bands or *trabeculæ*.

The **serous** coat is thin, smooth, and firmly adherent to the tunica propria beneath. It closely invests the surface of the organ, except at the places of its reflection to the stomach and diaphragm, and at the hilus.

Fig. 554.

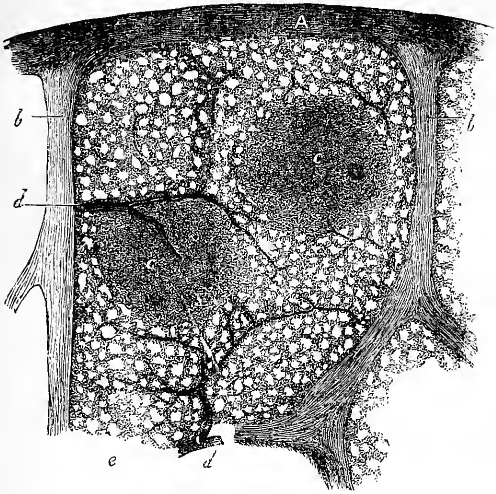


Fig. 554.—Vertical section of a small superficial portion of the human spleen (from Kölliker). Magnified with a low power.

A, peritoneal and fibrous covering; *b*, trabeculæ; *c c*, Malpighian corpuscles, in one of which an artery is seen cut transversely, in the other longitudinally; *d*, injected arterial twigs; *e*, spleen-pulp.

The **tunica propria** (fig. 554, A), much thicker and stronger than the serous coat, is whitish in colour and highly elastic. It is continuous with the trabecular structure within. Along the hilus this coat is reflected into the interior of the spleen, in the form of large trabeculæ, supported and enclosed by which run the blood-vessels and nerves; so that these are ensheathed by prolongations of the fibrous coat. These

Fig. 555.

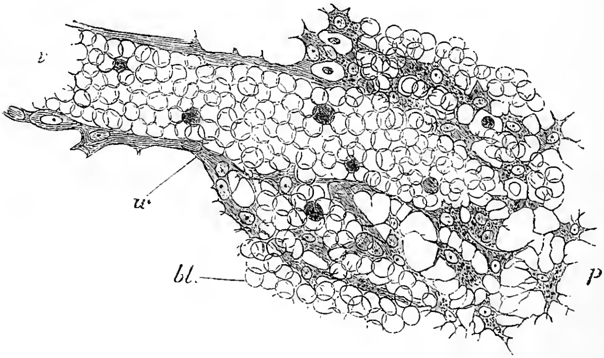


Fig. 555.—Thin section of spleen-pulp, highly magnified, showing the mode of origin of a small vein. (E.A.S.)

v, the vein, filled with blood-corpuscles, which are in continuity with others, *bl*, filling up the interstices of the retiform tissue of the pulp. At *p* the blood-corpuscles have been omitted from the figure, and the branched cells are better seen; *w*, wall of the vein. The shaded bodies amongst the red blood-corpuscles are pale corpuscles.

sheaths ramify with the vessels which they include, as far as their finer subdivisions, and are connected with numerous trabecular processes

which pass into the interior from the whole inner surface of the fibrous coat. The arrangement of the sheaths and trabeculæ may be easily displayed in the spleen of the ox by pressing and washing out the pulp from a section; and then they are seen to form a close reticulation through the substance. Thus, the proper coat, the sheaths of the vessels, and the trabeculæ, all of a highly elastic nature, constitute a distensible framework, which contains in its interstices or areolæ the red pulp. These fibrous structures are composed of interlaced bundles of areolar tissue containing a large amount of fine elastic tissue, and a few plain muscular fibre-cells. In the spleen of the pig, the dog, and the cat, and to a smaller extent in that of the ox and sheep, there is a far more abundant admixture of muscular tissue.

The **pulp** of the spleen is of a dark reddish-brown colour: when pressed out from between the trabeculæ it resembles grumous blood, and, like that, acquires a brighter hue on exposure to the air.

When a thin section which has been treated with solution of potash is examined under the microscope the pulp is seen to be everywhere pervaded by a reticulum of fine fibres, probably elastic, and continuous with the tissue of the trabeculæ. These fibres are in the natural condition covered over and concealed by branched connective-tissue corpuscles, which are of various forms and sizes; in some parts little but the intercommunicating branches remaining, in other parts the cells being larger and flatter and in closer connection (fig. 555, *p*). These corpuscles, which may be termed the *supporting cells of the pulp*, contain each a round or oval nucleus, like connective-tissue cells generally: and, in teased-out preparations of the fresh spleen substance it is not uncommon to find within them yellowish pigment granules of various sizes, presumably derived from blood-corpuscles. In the young subject the nuclei of many of these cells have been noticed to be multiple, or to be beset with prominences as if budding. The interstices between the sustentacular cells are, in sections of the hardened organ, always found to be occupied by blood (fig. 555, *bl*), white corpuscles occurring in rather larger proportion than in ordinary blood, especially in the neighbourhood of the Malpighian corpuscles to be immediately described. In close relation to the branched or flattened cells of the pulp, and occupying some of the smaller interstices between them, rounded, unbranched cells are seen, larger than white blood corpuscles, but otherwise much resembling them. These cells are amœboid and like the fixed cells of the pulp often contain both red blood corpuscles and clumps of pigment granules.

Blood-vessels.—The splenic artery and vein, alike remarkable for their great proportionate size, having entered the spleen by six or more branches, ramify in its interior, enclosed within the trabecular sheaths already described.

The smaller branches of the arteries leave the trabeculæ, and, passing into the proper substance of the spleen, divide into small tufts of arterioles arranged in pencils (fig. 556). But before they thus terminate, the adventitious fibrous coat which is prolonged over them from the trabeculæ becomes transformed into lymphoid tissue, which forms a comparatively thick sheath along each. This lymphoid sheath is abruptly dilated here and there into small oval or spheroidal enlargements, measuring on an average $\frac{1}{70}$ of an inch in diameter, but varying

in size from much smaller than this up to $\frac{1}{25}$th of an inch, and closely resembling the lymphoid follicles met with in the intestine and elsewhere. These lymphoid expansions may be seen on the surface of a fresh section of the organ as light-coloured spots scattered in the dark substance composing the pulp, and have been long noticed and described as the **Malpighian corpuscles** of the spleen (fig. 554, *c c*; fig. 556). In some cases the corpuscle is developed upon one side only of the arterial wall, upon which it then appears to be sessile; whilst in other instances—and this is the most frequent in the human subject—the expansion takes place all round the circumference of the vessel, by which it then appears to be pierced. In either case the artery sends off radiating branches to be distributed in the Malpighian corpuscle.

Fig. 556.

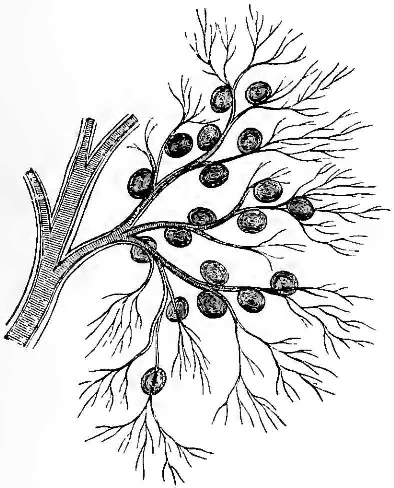


Fig. 556.—Small artery from the dog's spleen with Malpighian corpuscles attached. 10 Diameters (Kölliker).

As just stated, the Malpighian corpuscles are localized expansions of the lymphoid tissue of which the external coat of the smaller arteries of the spleen is formed. The reticulum of the tissue is comparatively open, being almost absent towards the centre of the corpuscle: at the confines it becomes closer; there is, however, no distinct boundary separating it from the retiform tissue of the pulp. The meshes are densely packed with lymphoid corpuscles, and the tissue is traversed by blood capillaries.

The small arteries terminate in capillaries, which after a longer or shorter course, lose their tubular character, the cells which compose their wall becoming partially separated from one another by elongated clefts; those at the extremity of the capillary acquiring processes and becoming united by these with the connective tissue cells of the pulp. In this manner their blood can flow directly into the interstices of the pulp tissue. The veins, which form a network of intercommunicating spaces within the pulp, commence in the same manner as the capillaries terminate; that is to say, the layer of flattened cells which lines and mainly composes their walls, on being traced back, loses its epithelioid character, and the cells, becoming thickened and spindle-shaped and their nuclei prominent, are found to be separated here and there from each other, and to be connected by processes with the cells of the pulp (fig. 555). The small veins take a different course from the arteries, for they soon pass to the trabeculæ and are conducted upon and within these, freely joining and anastomosing; whereas the arteries appear to have few or no anastomoses within the substance of the organ.

The small veins within the pulp of the human spleen often exhibit

peculiar transverse markings. These are produced by fine elastic fibres of the reticulum above described, which encircle the vessels.

From the description above given, it would appear that the blood in passing through the spleen is brought into immediate relation with the elements of the pulp, and no doubt undergoes important changes in the passage; in this respect resembling the lymph as it passes through the lymphatic glands. Two modifications which are probably effected in it may be here pointed out. In the first place the lymphoid tissue ensheathing the arteries, together with that composing the Malpighian corpuscles, would appear, like the same tissue in the lymphatic glands, and other parts, to be the seat of the production of pale blood corpuscles. At the circumference of this tissue, these may pass into the interstices of the pulp, and so into the blood. It is found, in fact, that the blood of the splenic vein is extremely rich in pale corpuscles. In the second place, red blood-corpuscles may be taken up by the pulp-cells, their colouring matter being transformed into pigment. The splenic cells have, indeed, been noticed, when examined on the warm stage, to take red corpuscles, which were in contact with them, into their interior.

The **lymphatics** of the spleen form two systems, a *trabecular* and a *perivascular*. The vessels belonging to the former run in the trabeculæ and are in communication with a superficial network in the capsule. The perivascular take origin in the interstices of the lymphoid tissue which ensheaths the smaller arteries, and which forms the Malpighian corpuscles; they do not, therefore, at first form distinct vessels. When these are seen they commonly run in pairs, one on either side of an artery, uniting over it by frequent anastomoses, and sometimes partially or wholly enclosing it. At the hilus the two sets of lymphatics join and proceed along the gastro-splenic omentum to the neighbouring lymphatic glands.

The **nerves**, derived from the solar plexus, surround and accompany the splenic artery and its branches. They are most probably distributed to the vessels and plain muscular tissue of the framework.

Literature.—*Gray*, Structure and Use of the Spleen, 1854; *Busk and Huxley* on the Malpighian Bodies, in the Sydenham Society's translation of Kölliker's Histology; also *Huxley*, in Micro. Jour., II., p. 74; *Billroth*, in Zeitschrift f. wiss. Zoologie, XI., and Virch. Arch. XX., 1861; and XXIII., 1862; *W. Müller*, Ueber d. fein. Bau der Milz, 1865, and in Stricker's Handbook; *Stieda*, in Virch. Arch., XXIV.; *Schweigger-Seidel*, Virch. Arch. XXVII., 1863; *Tomsa*, Wiener Sitzungsb. XLVIII., 1864; *Peremeschko*, in Wiener Sitzungsb. 55, 1870; *Wedl*, Wiener Sitzungsb. 64, 1871; *Kyber*, Arch. f. mikr. Anat. VI., 1870, and VIII., 1872; *Rindfleisch* in Berlin, klin. Wochenschr., 1872; *M. Schultze*, in the same journal; *Stoff u. Hasse* in Med. Centralbl., 1872; *Klein* in the Quart. Journ. of Micro. Sci., 1870.

SUPRARENAL BODIES.

The *suprarenal bodies* or *capsules* (*capsulæ atrabilariæ seu renes succenturiati* of old anatomists), are two flattened bodies, belonging to the class of organs formerly known as ductless glands, each of which surmounts the corresponding kidney (fig. 557). The upper border of the right capsule, convex and thin, is often considerably elevated in the middle so as to give the body a triangular form. The lower border is concave, and rests upon the anterior and inner part of the summit of the kidney, to which it is connected by loose areolar tissue: it is thick, and almost always deeply grooved. The posterior surface rests upon the diaphragm. The anterior surface presents an irregular fissure named the *hilus*, from which the suprarenal vein emerges (fig. 558, *v*). The right capsule is pyramidal in shape and projects more above the

kidney than the left. It is covered by the liver (at the impressio suprarenalis). The left capsule is more crescentic in form and is generally larger than the right. In most cases it only just projects above the kidney. The concave border rests against the convex inner border of the head of the kidney. It is in contact below with the pancreas, above and externally with the spleen. Its posterior surface rests against the left crus of the diaphragm; its anterior surface is covered by the stomach and pancreas.

Fig. 557.

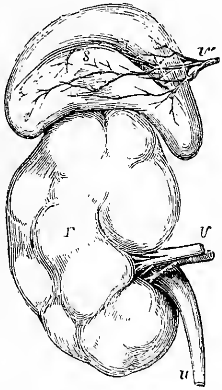


Fig. 558.

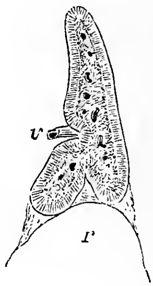


Fig. 557.—Front view of the right kidney and suprarenal body of a full-grown fœtus (Allen Thomson).

This figure shows the lobulated form of the fœtal kidney, *r*; *v*, the renal vein and artery; *u*, the ureter; *s*, the suprarenal capsule, the letter is placed near the sulcus in which the large veins (*v'*) are seen emerging from the interior of the organ.

Fig. 558.—Section of the suprarenal body (Allen Thomson).

A vertical section of the suprarenal body of a fœtus, twice the natural size, showing the lower notch by which it rests on the summit of the kidney, and the anterior notch by which the veins issue, together with the distinction between the medullary and cortical substance.

The suprarenal capsules measure from an inch and a quarter to an inch and three-quarters from above down, and about an inch and a quarter from side to side; their thickness is from one-sixth to one-quarter of an inch. The *weight* of each in the adult is from one to two drachms.

Structure.—Besides a covering of areolar tissue mixed frequently with much fat, the suprarenal capsules have a thin fibrous investment. On the exterior their colour is yellowish or brownish-yellow. When divided (fig. 558), they are seen to consist of two substances: one, *external* or *cortical*, is of a deep yellow colour, firm and striated, and forms the principal mass of the organ; the other, *internal* or *medullary*, is in the adult of a dark brownish-black hue, and so soft and pulpy that some anatomists have erroneously described a cavity within it.

The **fibrous investment** (fig. 559, *a*), which is distinguishable into

an outer looser and an inner firmer part, is so intimately connected with the deeper parts that it cannot be removed without lacerating the subjacent structure. Its deeper layers contain plain muscular cells, at least in some animals: it is continuous with the septa which enter into the formation of the substance of the organ.

Fig. 559.

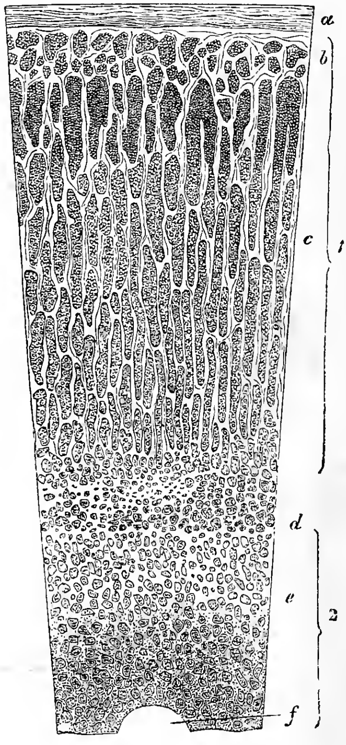


Fig. 559.—Vertical section of suprarenal body: human. Magnified (Eberth).

1, cortical substance; 2, medullary substance: *a*, capsule; *b*, zona glomerulosa; *c*, zona fasciculata; *d*, zona reticularis; *e*, groups of medullary cells; *f*, section of a large vein.

The **cortical part** of the suprarenal body, examined in a section with a low magnifying power (fig. 559, 1), is seen to consist of a fibrous stroma, in which are imbedded column-like, intercommunicating groups of cells (*c*). The groups measure on an average $\frac{1}{700}$th of an inch in diameter, and are arranged vertically to the surface of the organ. In the deepest part of the cortex, however, the colour is darker, and the columnar arrangement is lost, the stroma being more equally distributed (*d*); and immediately beneath the fibrous coat there is another narrow zone in which the stroma encloses what in section look like rounded or oval spaces occupied by groups of cells, which are really the outer ends of the columnar groups above mentioned (*b*).

These inner and outer layers have been named by J. Arnold respectively zona reticularis and zona glomerulosa, while he applies the term zona fasciculata to the main part (*c*); but the transition from one of these parts to another is not sudden nor indicated by any line of demarcation.

The cells which form the groups and columns of the cortical substance are polyhedral in form (fig. 560): their protoplasm is finely reticular, and not unfrequently contains yellowish oil globules. The cells vary from $\frac{1}{2000}$th to $\frac{1}{1350}$th of an inch in size: each has a clear round nucleus.

In some animals (horse, dog), the spaces of the zona glomerulosa are occupied by regularly arranged long columnar cells, set around a sort of lumen, and looking not unlike part of a glandular tube. In man, however, most of the cells of this part are polyhedral, like those of the other zones.

The small arteries, entering from the surface, run in the septa parallel to the columns, frequently anastomosing together between them, and surrounding each

group of cells with a fine capillary network. Small bundles of nerves pass inwards in the septa between the columns to reach the medullary part of the organ and their fibres begin to spread out in the zona reticularis, but do not appear to be distributed to the cortical substance.

Lymphatics run in the trabeculæ of the cortical substance and are connected with cleft-like spaces between the trabeculæ and the cell-columns, and even with fine clefts between the cells within the columns (Klein). They communicate with efferent valved lymphatics both in the fibrous coat and in the medulla around the central vein.

The **medullary part** (fig. 559, 2) of the suprarenal capsule is marked off from the cortical part by a layer of loose connective tissue. In the thinner parts of the adult organ there is no medullary part, and the layer of connective tissue referred to is found separating the deep surfaces of two

Fig. 560.

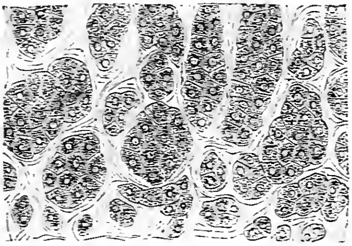


Fig. 561.

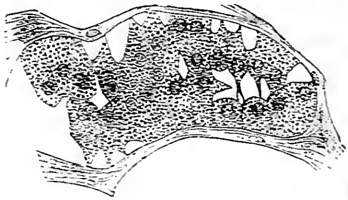


Fig. 560.—Cells and cell-groups from the outermost layer of the cortical substance of the suprarenal body. Highly magnified (Eberth).

Fig. 561.—A small portion of the medullary part of the suprarenal capsule of the ox (Eberth). Highly magnified.

opposed portions of the cortical part; but in the young state the distinction of cortical and medullary portions probably extends throughout the whole gland. The medullary part is pervaded by large venous capillaries, which receive the whole of the blood which has passed through the organ. These venous capillaries are supported by the fibrous stroma, which also contains, especially in man, a number of bundles of plain muscular cells disposed parallel to the course of the larger veins, and forming a complete investment to the issuing suprarenal vein (v. Brunn). The general arrangement of the stroma is reticular; in its meshes are enclosed groups of cells (fig. 561), which differ from those of the cortex in being more irregular in form, of a clearer aspect and destitute of oil-globules. Moreover they become stained of a deep brown colour, by solutions of bichromate of potash, whereas the cortical cells are but slightly tinged by that re-agent.

In some animals the medullary cells contain a large amount of reddish-brown pigment, but this is not generally the case in the human subject, the deep colour of the medulla being chiefly due to the blood within its numerous vessels.

The bundles of nerves which pass through the cortical substance run between it and the medullary substance, and then form a copious interlacement which extends through the whole medullary stroma. Indeed,

some observers (Leydig and Luschka) have regarded the cells of the medullary substance as nerve-cells. Moers and others describe ganglion-cells on the nervous plexuses in the medulla, and there are also ganglia on the nerves which ramify in the fibrous investment (Henle). The medullary substance receives its blood by the continuation inwards of the capillary network of the cortex. The blood is collected by venous radicles which open into the stems in the centre of the organ and these emerge at the hilus.

Vessels.—The suprarenal bodies receive *arteries* from three sources, viz., from the aorta, the phrenic, and the renal arteries.

The *veins*, which pass out from the centre, are usually united into one for each organ. The right vein enters the vena cava inferior immediately, whilst the left, after a longer course, terminates in the left renal vein.

Nerves.—The nerves which are exceedingly numerous are derived from the solar plexus of the sympathetic, and from the renal plexuses. According to Bergmann, some filaments come from the phrenic and pneumogastric nerves. They are made up mainly of medullated fibres, of different sizes, and they have many small ganglia upon them before entering the organ. The nerves are especially numerous in the lower half, and inner border.

Accessory suprarenal capsules are occasionally met with, attached by connective tissue to the main bodies; and varying from a small size up to that of a pea. According to Duckworth they possess no medullary part.

Function.—Nothing is known positively with regard to the function of the suprarenal capsules. The opinion which has met with most acceptance among physiologists is that these bodies belong to the class of blood-vascular glands, and exert some influence upon the elaboration or disintegration of nutritive material. The product of the cell-activity, whatever it may be, is believed by Klein to be carried off by the lymphatics of the organ, as in the analogous case of the thyroid body. Bergmann, however, who was the first to point out the richness of their nervous supply, suggested that they were parts of the sympathetic nervous system, and in this opinion he has been followed by Leydig and Luschka. A bronzed tint of skin, together with progressive emaciation and loss of strength, is frequently found in conjunction with various forms of disease more or less involving and altering the structure of these bodies (Addison's disease).

Literature.—*Bergmann*, Inaug. Diss., Göttingen, 1839; *Ecker*, Der feinere Bau der Nebennieren, &c., 1846; *Frey*, Article in Todd's Cyclopædia, 1849; *G. Harley* in the Lancet, 1858; *Moers* in Virch. Arch., 1864; *Duckworth* in St. Barthol. Hosp. Reports, 1865; *Holm* in Wiener Sitzungsb., 1866; *Grandry* in Journ. de l'anat., 1867; *Eberth* in Stricker's Handbook, 1871; v. *Brunn* in Arch. f. mikr. Anat., VIII.; and Göttinger Nachr., 1873; *Creighton* in Proc. R. S., 1877 and Journal of Anat. and Phys., XIII.; *Mitsukuri* in Quarterly Journ. of Micro. Sci., 1882.

THE URINARY ORGANS.

The urinary organs consist of the *kidneys*, the glands by which the urine is secreted, and the *ureters*, *bladder*, and *urethra*, serving for its reception and evacuation.

THE KIDNEYS.

The *kidneys*, two in number, are deeply seated in the loins, lying one on each side of the vertebral column, at the back part of the abdominal cavity, and behind the peritoneum. They are on a level with the last dorsal and the two or three upper lumbar vertebræ, the right kidney being usually a little lower than the left, probably in consequence of the vicinity of the large right lobe of the liver. They

are maintained in this position by their vessels, and by a quantity of surrounding loose areolar tissue, which usually contains much fat (tunica adiposa).

Fig. 562.

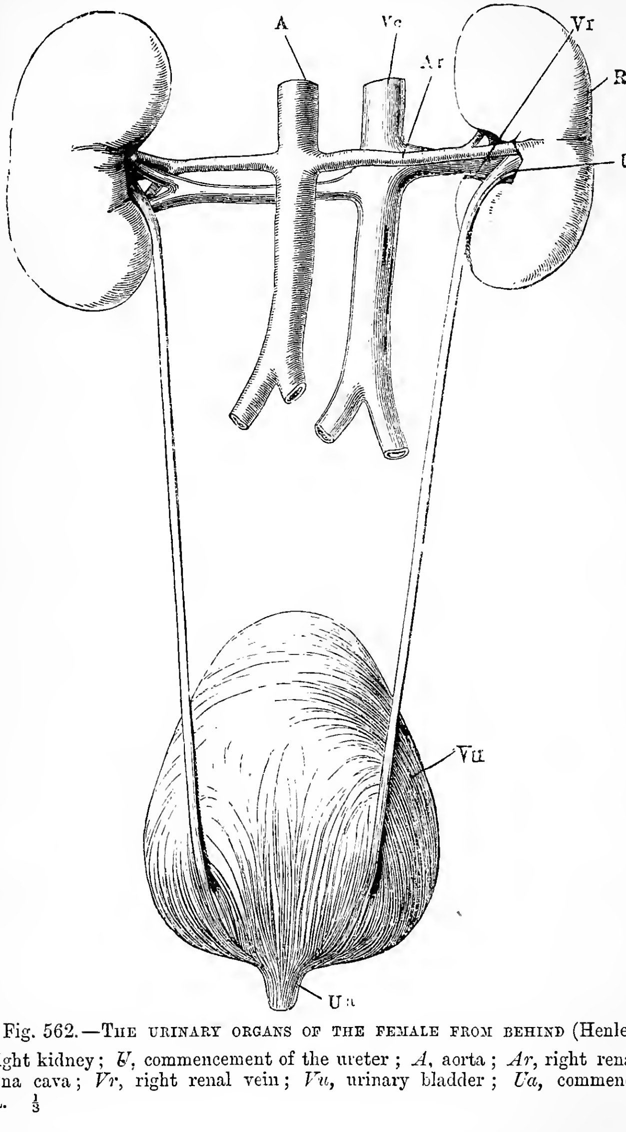


Fig. 562.—The urinary organs of the female from behind (Henle).

R, right kidney; *U*, commencement of the ureter; *A*, aorta; *Ar*, right renal artery; *Vc*, vena cava; *Vr*, right renal vein; *Vu*, urinary bladder; *Ua*, commencement of urethra. $\frac{1}{3}$

The kidneys measure about 4 inches in length, $2\frac{1}{2}$ inches in breadth, and $1\frac{1}{4}$ inch or more in thickness. The left is usually longer and narrower than the right. The weight of the kidney is usually stated to be about $4\frac{1}{2}$ oz. in the male, and somewhat less in the female.

Form and Connections.—The surface of the kidney is smooth, and of a deep red colour. Its form is peculiar: it is compressed from before backwards with a convex outer, and concave inner border, and somewhat enlarged extremities, the upper extremity being set somewhat further back than the lower.

The *anterior surface*, more convex than the posterior, looks somewhat outwards, and is partially covered at its upper end by the peritoneum. The duodenum and commencement of the transverse colon, both destitute of peritoneum behind, are in contact with the anterior surface of the right kidney, and the descending colon with that of the left. The front of the right kidney, moreover, touches the under surface of the liver, and that of the left the fundus of the stomach, the latter producing a slight concave impression on the kidney. Below, the anterior surface of the left kidney comes in contact with the pancreas. The *posterior surface*, imbedded in areolar tissue, rests firstly upon the lower part of the arch of the diaphragm, in front of and below the twelfth rib; secondly, on the anterior layer of lumbar fascia, covering the quadratus lumborum muscle; and, lastly, on the psoas muscle which corresponds with a shallow concave impression on the posterior surface of the organ. The *external border*, convex in its general outline, is directed somewhat backwards towards the wall of the abdomen. On the left side it is in contact for the upper two-thirds of its extent with the spleen. The *internal border*, concave and deeply excavated towards the middle, is directed a little downwards and forwards. It exhibits a longitudinal *fissure* bounded by an anterior and posterior lip, and named the *hilus of the kidney*, at which the vessels, the excretory duct, and the nerves enter or pass out. In this hilus, the renal vein lies in front, the artery and its branches next, and the expanded excretory duct or ureter behind and towards the lower part. The *upper end* of the kidney, which is larger than the lower, is thick and rounded, and supports the suprarenal capsule, which descends a little way upon its anterior surface. This end of the kidney reaches, on the left side, to about the upper border of the twelfth dorsal vertebra, and on the right, half an inch lower. It is moreover directed slightly inwards, so that the upper ends of the two kidneys are nearer to each other than the lower ends, which are smaller and somewhat flattened, diverge slightly from the spine, and reach nearly as low as the crest of the ilium.

Varieties.—The kidneys are sometimes longer and narrower, and sometimes shorter and more rounded than usual. Occasionally one kidney is very small whilst the other is proportionately enlarged. They may be situated lower down than usual, even in the pelvis.

Instances are now and then met with in which the two kidneys are joined by their lower ends across the front of the great blood-vessels and vertebral column. The conjunct organ has usually the form of a horse-shoe. Sometimes two united kidneys are situated on one or other side of the vertebral column, in the lumbar region, or, but much more rarely, in the cavity of the pelvis. In other very rare cases three glandular masses have been found, the supernumerary organ being placed either in front or on one side of the vertebral column, or in the pelvic cavity.

Structure.—The kidney is surrounded by a proper fibrous coat, which forms a thin, smooth, but firm investment, closely covering the organ. It consists of dense areolar tissue, with numerous fine elastic fibres, and can easily be detached from the substance of the gland, to which it adheres by minute processes of connective tissue and

vessels. Underneath the capsule in the human kidney is an incomplete layer of plain muscular fibres.

On splitting open the kidney by a longitudinal section, from its outer to its inner border, the fissure named the hilus (fig. 563, *h, h*) is found to extend some distance into the interior of the organ, forming a cavity called the *sinus* of the kidney (*s*). This is enclosed on all sides except at the hilus by the solid substance of the organ; and is lined by an inward prolongation of the fibrous coat. The solid part consists of *cortical* and *medullary* substance; the latter being arranged in separate conical masses named "pyramids of Malpighi," with their broad bases (*b, b*) directed towards the surface, and their points towards the sinus, where they form prominent *papillæ*. The pyramids are imbedded in the cortical substance, which separates them from each other, and encloses them everywhere except at the papillæ, which emerge from it and project into the sinus.

The external or cortical substance (*a*) is situated immediately within the fibrous capsule, and forms the superficial part of the organ through-

Fig. 563.

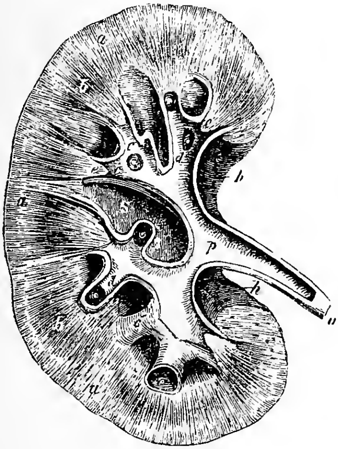


Fig. 563.—Plan of a longitudinal section through the pelvis and substance of the right kidney. One-half the natural size.

a, the cortical substance; *b, b*, broad part of two of the pyramids of Malpighi; *c, c*, the divisions of the pelvis named calices, or infundibula, laid open; *c'*, one of these unopened; *d, d*, summit of the pyramids or papillæ projecting into calices; *e, e*, section of the narrow part of two pyramids near the calices; *p*, pelvis or enlarged portion of the ureter within the kidney; *u*, the ureter; *s*, the sinus; *h*, the hilus.

out its whole extent to the depth of about two lines, and moreover sends prolongations inwards (*septula renum*, or *columnæ Bertini*) between the pyramids as far as the sinus and bases of the papillæ. It is of a nearly uniform light crimson brown appearance, and is soft and easily lacerated in directions vertical to the surface. The medullary portion of the kidney is more dense than the cortical, and is distinctly striated, owing to its consisting of small diverging uriniferous tubes, and to its blood-vessels being arranged in a similar manner. There are generally more than twelve pyramids, but their number is inconstant, varying from eight to eighteen. Towards the papillæ the pyramids are of a lighter colour than the cortical substance, but at their base they are usually purplish and darker.

Excretory apparatus.—On squeezing a fresh kidney which has been split open, a little urine will be seen to drain from the papillæ by fine orifices on their surface. The secretion is carried away and conveyed into the bladder by the ureter. This long tube on being traced up to the kidney is seen to be somewhat enlarged, and then to expand as it enters the fissure, into a large funnel-shaped dilatation named the

pelvis (fig. 546, P). This within the sinus, divides usually into three, but sometimes only two primary tubular divisions, and these at length end in a larger number of short, truncated but comparatively wide branches named *calices* or *infundibula*, which receive the papillæ into their wide mouths and are attached around the bases of those prominences from which, of course, they catch the issuing urine.

Fig. 564.

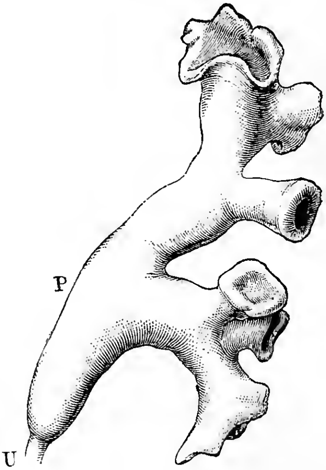


Fig. 564.—Cast of the interior of the upper end of the ureter (Henle).

P, pelvis; *U*, ureter.

A single calix often surrounds two, sometimes even three papillæ, which are in that case united together; hence, the calices are in general not so numerous as the papillæ. The spaces between the calices are occupied by a considerable amount of fat, imbedded in which are seen the main branches of the renal vessels.

Like the rest of the ureter, the pelvis and greater part of the calices consist of three coats, viz., a strong external fibrous and elastic tunic, which becomes continuous around the bases of the papillæ with that part of the proper coat of the kidney which is continued into the sinus; secondly, a thin internal mucous coat, which, or at least its epithelium, is reflected over the summit of each papilla; and thirdly, between these two, a double layer of muscular fibres, longitudinal and circular. The longitudinal fibres are lost near the extremity of the calix, but the circular fibres, according to Henle, form a continuous circular muscle round the papilla where the wall of the calix is attached to it.

The pyramidal masses found in the adult kidney indicate the original separation of this gland into lobules in the earlier stages of its growth. Each of these primitive lobules is in fact a pyramid surrounded by a proper investment of cortical substance, and is analogous to one of the lobules of the divided kidneys seen in many of the lower animals. As the human kidney continues to be developed, the adjacent surfaces of the lobules coalesce and the gland becomes a single mass; the contiguous parts of the originally separate cortical investments, being blended together, form the partitions between the pyramids already described. Moreover, upon the surface of the kidney even in the adult, after the removal of the fibrous capsule, faintly marked furrows may be traced on the cortical substance, opposite the intervals in the interior between the several Malpighian pyramids; and not unfrequently instances occur in which a deeper separation of the original lobules by grooves remains apparent in the adult kidney.

Tubuli uriniferi.—On examining the summit of one of the papillæ carefully, especially with the aid of a lens, a number of small orifices may be seen varying in diameter from $\frac{1}{300}$th to $\frac{1}{200}$th of an inch. They are frequently collected in large numbers at the bottom of a slight depression or *foveola* found near the summit of the papilla, but most commonly the surface is pitted over with about a score of small de-

pressions of this sort. On tracing these minute openings into the substance of the pyramids, they are discovered to be the mouths of small tubes or ducts, the *uriniferous tubes* before mentioned, which thus open upon the surface of the several papillæ into the interior of the calices.

As these tubuli pass up into the pyramidal substance, they bifurcate again and again at very acute angles, their successive branches running close together in straight and slightly diverging lines, and they continue thus to divide and subdivide until they reach the sides and bases of the pyramids, whence they pass, greatly augmented in number into the cortical substance. In the cortical part the straight tubules belonging to a Malpighian pyramid are continued for some way, in several groups or bundles, the tubules in the centre of which approach nearer the surface than those at the sides. These bundles are known as the *medullary rays* (fig. 565, *m*) of the cortex, and the cortical substance between and around them is termed, on account of the intricate arrangement of its tubules, the *labyrinth of the cortex*.

Fig. 565.

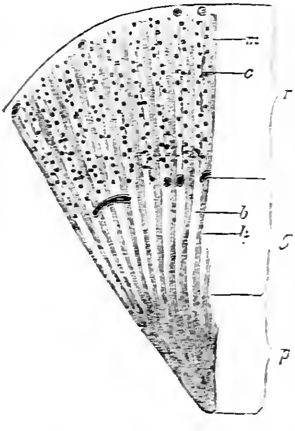


Fig. 565.—Section through part of the dog's kidney (Ludwig).

p, papillary and *g*, boundary zones of the medulla; *r*, cortical layer; *h*, bundles of tubules in the boundary layer, separated by spaces, *b*, containing bunches of vessels (not here represented), and prolonged into the cortex as the medullary rays, *m*; *c*, intervals of cortex, composed chiefly of convoluted tubules, with irregular rows of glomeruli, between the medullary rays.

The part of the pyramid which is nearest the cortical substance contains a number of pencil-like bundles of small blood-vessels, which originating from arterial and venous arches at the junction of cortex and medulla, dip into the pyramid, and thus commence the separation of its tubules into the bundles which are continued into the cortex as the medullary rays. The portion of the pyramid which is thus broken up is termed the *boundary zone* (fig. 565, *g*).

Course of the tubules.—The tubes commence in the labyrinth of the cortical substance by spherical dilatations enclosing like a capsule the vascular Malpighian tufts to be afterwards described.

Emerging from this dilatation (fig. 566, 1), which is known as the *capsule*, by a narrow neck (2), the tubule is at first convoluted and wide (*first convoluted tubule*), but on approaching the medullary ray it becomes nearly straight with a slight tendency to a spiral (*spiral tubule* of Schachowa, 4). At the junction of cortex and medulla the spiral tube rapidly narrows and passes straight down through the boundary zone towards the apex of the pyramid. After a shorter or longer course, however, it loops upwards again (6) becoming enlarged in the boundary zone (7), but somewhat smaller again above this (8, 9) where it passes again up the medullary ray. The part of the uriniferous tube which thus dips down towards the papilla and turns upwards again is known as the *looped tubule of Henle*. On emerging from the medullary ray the tubule is

characterized by great irregularity of outline (*irregular tubule*, 10) before again becoming convoluted (*second convoluted tubule*, 11). Finally this last is connected with one of the collecting tubules of the medullary ray by a small *junctional tubule* (12), and the *collecting tubes* (13,

Fig. 566.

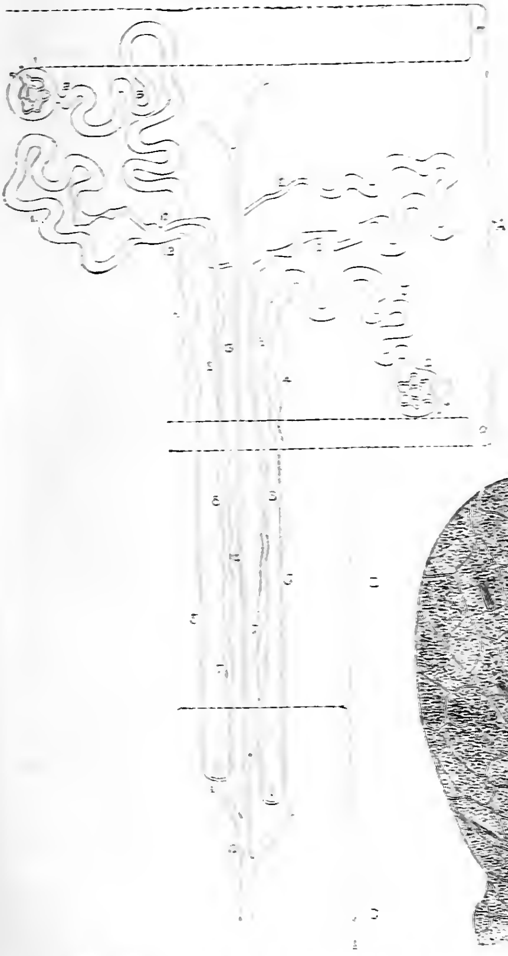


Fig. 567.

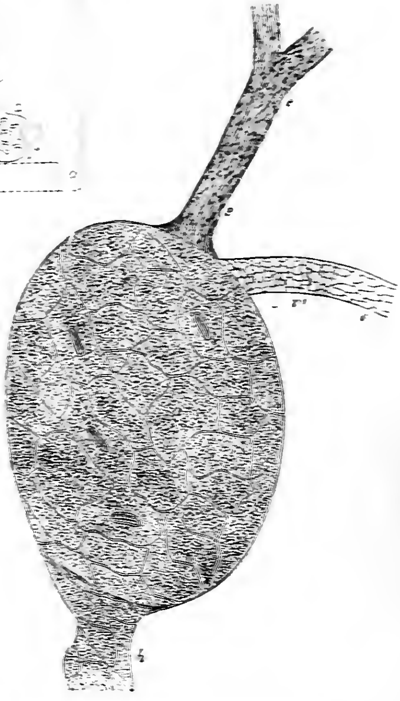


Fig. 566.—Diagram of the course of two uriniferous tubules (Klein).

A, cortex; B, boundary, zone C, papillary zone of the medulla: *a*, *a'*, superficial and deep layers of cortex, free from glomeruli. For the explanation of the numerals, see the text.

Fig. 567.—Malpighian corpuscle from the rabbit's kidney: nitrate of silver preparation. Highly magnified (Ludwig).

v, vas afferens, showing its epithelial lining: at *v'*, the transverse muscular fibres are also seen; *e*, vas efferens; *a*, *a'*, basement membrane of capsule with epithelioid markings, passing at *h* into that of the commencing uniferous tubule.

14, 15) uniting with one another, as already noticed, become gradually larger as they pass to open as *excretory tubes* at the summit of the papilla.

Structure of the tubules.—The tubules consist in every case of a

Fig. 568.

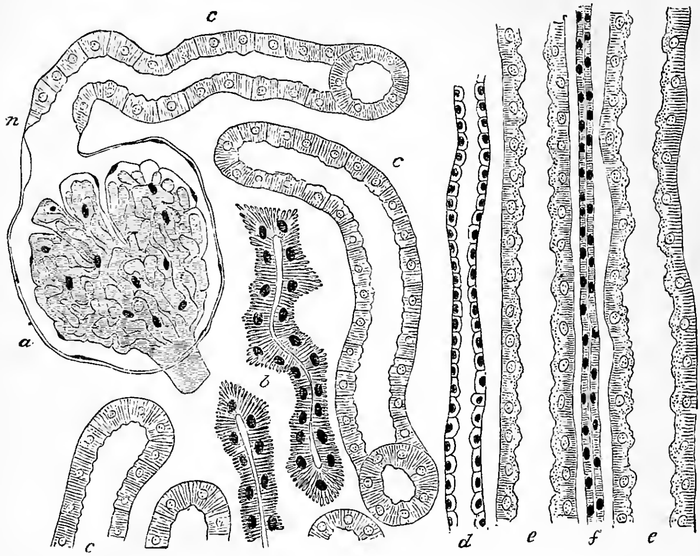


Fig 568.—Tubules from a section of the dog's kidney (Klein and Noble Smith).

a, Capsule, enclosing the glomerulus; *n*, neck of the capsule; *c*, *c*, convoluted tubules; *b*, irregular tubules; *d*, collecting tube; *e*, *e*, spiral tubes; *f*, part of the ascending limb of Henle's loop, here (in the medullary ray) narrow.

basement membrane and epithelium, but the character of the latter as well as the size of the tubes varies considerably in the different parts.

Fig. 569.

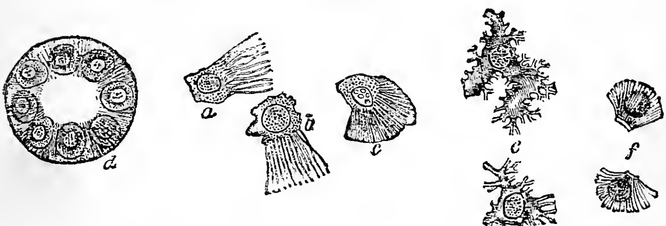


Fig. 569.—To illustrate the structure of the epithelium of the convoluted tubules (from Heidenhain).

d, section of a convoluted tubule from the rat, showing the unaltered protoplasm occupying a circular area around the nucleus of each cell; *a*, *b*, *c*, isolated cells from the convoluted tubules of the rat; *c*, isolated cells from the dog's kidney, viewed from the inner surface, and showing the irregular contour of the protoplasm; *e*, *f*, isolated cells from the newt, showing the rods and the homogeneous cuticular layer.

Fig. 570.

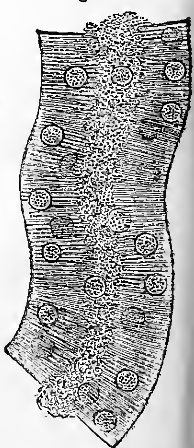


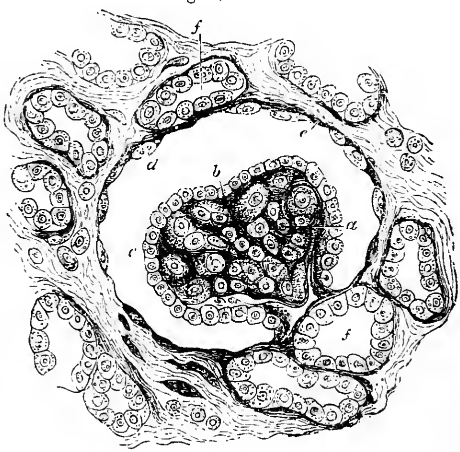
Fig. 570.—Part of a convoluted tubule of the dog's kidney (Heidenhain).

The *capsule* (fig. 568, *a*), is lined by a layer of flattened cells, which is reflected over the contained tuft of blood-vessels, dipping between the separate bunches of which this is composed. This layer is much more easily recognized in the fœtus and young subject than in the adult (fig. 571). At the *neck* the epithelium becomes cubical. It has been shown by Hassall in the sheep, horse, and rabbit, and more recently by Klein in the mouse, that the epithelium here is provided with cilia, and it is not improbable that the same may be the case in all mammals. In lower vertebrates as in the frog, the existence of cilia in this place has long been known. The *first convoluted tubule* has an epithelium of a peculiar character (Heidenhain). The part of the cell which encloses the nucleus is composed of ordinary granular-looking protoplasm, but the part next the basement membrane is chiefly made up of straight or nearly straight rods or fibrils placed vertically to the basement membrane and extending a variable distance towards the lumen (figs. 569, 570), but usually occupying the greater part of the cell,

Fig. 571.—Section of cortical substance of kidney: human fœtus. Highly magnified (Klein).

a, glomerulus with blood-vessels not fully developed; *c*, epithelium covering it continuous with *d*, flattened epithelium lining Bowman's capsule; *f*, *f*, convoluted tubes.

Fig. 571.



although there is always a stratum of homogeneous substance bounding the cell towards the lumen (fig. 569, *f*). The nucleus is spherical. The cells are with difficulty separated from one another, at least in some animals (*e.g.*, dog) owing to the cells possessing lateral ridge-like processes (fig. 569, *e*) which interlock with one another (Schachowa). The *spiral tubule* of Schachowa is the continuation of the convoluted tubule into the medullary ray, and possesses a similar epithelium (fig. 568, *e*). Towards its termination, however, the cells become shorter and less distinctly fibrillated, but split up more completely into lateral ridges with intervening furrows, especially in the part of the cell next the basement membrane, so that the cells bear somewhat the aspect of columns deeply fluted at their base. Between these fluted cells, others of clearer aspect are found fitting in, and having an expanded base which extends partly underneath them. According to Schachowa they are present also in the convoluted tubules proper.

In the narrow tube which forms the *descending limb of Henle's loop*, and in the loop itself, the epithelium is quite low, and flattened against the basement membrane. The protoplasm is clear and the nucleus prominent. The ridge-like processes at the base of the cells are said not to be altogether absent even here.

In the *ascending limb* of the looped tubule the epithelium again takes

on the character which is exhibited in the first convoluted and spiral tubes, but the cells are rather smaller, the lumen of the tube relatively larger, and the intracellular rods not so long as in those tubes. The cells of this segment are sometimes set obliquely so as to overlap one another. In the human subject they contain brown pigment-granules (Klein).

In the *irregular tubules* on the other hand the rod-like structure of the cells is very distinct (fig. 568, *b*). The cells are very unequal in size, the irregularity of the tubules being thus compensated, and the lumen rendered nearly the same throughout. The nucleus is oval.

The *second convoluted tubule* (intercalary tube of Schweigger-Seidel) is like the first in size, but has a different kind of epithelium. The cells, which are rather long, with a relatively large nucleus, present a peculiar highly refractive appearance, and where they rest on the membrana propria, the protoplasm exhibits projections which fit between those of neighbouring cells.

The *junctional tubule,* which unites the last-named to the collecting tubes, is narrow, but its lumen is relatively large. It is lined by clear flattened or cubical cells ; but between them some cells are found which are similar in appearance to the cells which line the segment just described.

The *collecting tubes,* which are characterised by their straight course and very distinct lumen (fig. 568, *d*) are lined by a clear cubical epithelium, the cells of which are at first somewhat irregular, but become longer and more regular as the tubes approach the papilla, so that in the larger collecting or *excretory tubes* the form of the cells is typically columnar, modified only by the form of the surface which they cover. In these largest tubes the basement membrane is said to be absent, the epithelium cells resting directly upon the connective tissue.

Klein describes a very delicate nucleated membrane lining the tubules within the epithelium, in all the tubes except the descending limb of Henle's loop, and in the loop itself.

Blood-vessels.—The kidneys are highly vascular, and receive their blood from the renal arteries, which are very large in proportion to the size of the organs they supply. Each renal artery divides into four or five branches, which, passing in at the hilus, between the vein and ureter, may be traced into the sinus of the kidney, where they lie amongst the infundibula, together with which they are usually embedded in a quantity of fat. Penetrating the substance of the organ between the papillæ, the arterial branches enter the cortical substance which intervenes between the pyramids of Malpighi, and proceed in this, accompanied by a sheathing of areolar tissue, and dividing and subdividing, to reach the bases of the pyramids, where they form arches between the cortical and medullary parts, which however are not complete, and in this respect differ from the freely anastomosing venous arches which accompany them. From the arches smaller "interlobular" arteries (fig. 572, *ai*) are given off, which pass outwards between the medullary rays and amongst the convoluted tubules, pursuing a nearly straight course towards the surface of the organ. As they proceed they give off at intervals short and usually curved branches which proceed without further division to the dilated ends of the uriniferous tubules. Within the capsule the small artery

(afferent vessel) breaks up into a larger number of capillary vessels which have a convoluted arrangement, and are closely held together by connective tissue to form a spheroidal vascular tuft, the *glomerulus*

Fig. 572.

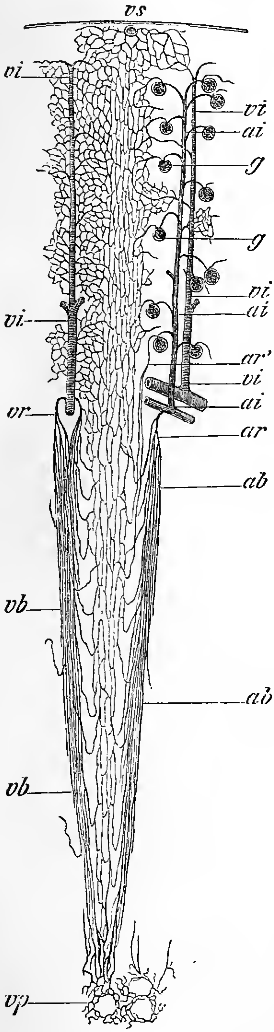


Fig. 573.

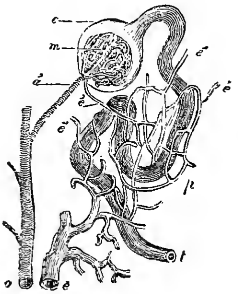


Fig. 572.—Diagram of the distribution of the blood-vessels in the kidney (from Ludwig).

ai, *ai*, interlobular arteries; *vi*, *vi*, interlobular veins; *g*, a glomerulus; *vs*, stellate vein; *ar*, *vr*, arteriæ et venæ rectæ forming pencil-like bundles, *ab*, *vb*; *vp*, venous plexus in the papillæ.

Fig. 573.—Diagram showing the relation of the uriniferous tubules to the blood-vessels (after Bowman).

a, one of the interlobular arteries; *a'*, afferent artery passing into the glomerulus; *c*, capsule of the glomerulus; *t*, convoluted tube; *e'*, *e'*, efferent vessels which subdivide in the plexus *p*, surrounding the tube, and finally terminate in the interlobular vein, *e*.

of Malpighi. A vein (efferent vessel) smaller than the artery, emerges from the glomerulus close to the point where the artery enters; but, instead of joining with other small veins to form larger venous trunks, as is the case in other organs, the efferent vessel divides into branches after the manner of an artery, and from these arises a dense network of capillaries which everywhere ramify over the walls of the uriniferous tubules (fig. 573), the meshes of the network being polygonal amongst the convoluted tubules and elongated amongst the tubules of the medullary rays. But the efferent vessels from the lowermost glomeruli break up wholly into pencils of straight vessels (false vasa recta) which pass directly into the boundary layer of the medulla, and there supply the continuation downwards of the medullary rays into the pyramid.

The renal arteries give branches likewise to the capsule of the kidney which anastomose with branches of the lumbar arteries, and that so freely that Ludwig was able partially to inject the kidneys of a dog from the aorta after the renal arteries had been tied.

The blood is conveyed from the cortex of the kidney by *interlobular veins* which accompany the interlobular arteries, and join the convex side of the venous arches which lie between the medulla and cortex, and also by veins which lie close beneath the capsule of the organ, and take

Fig. 574.

Fig. 575.

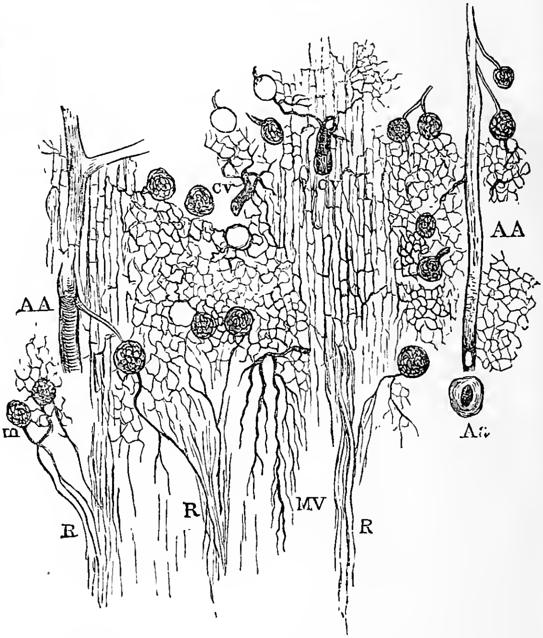


Fig. 574.—Injected glomerulus from the inner part of the cortical substance of the horse's kidney. 70 diameters (from Kölliker after Bowman).

a, interlobular artery; *af*, afferent vessel; *m*, *m*, convoluted vessels of the glomerulus; *e f*, efferent vessel; *b*, its subdivision in the medullary substance.

Fig. 575.—Longitudinal section of a part of the medullary substance and the adjacent cortical substance of the kidney, showing the blood-vessels injected (from Southey).

The figure is designed principally to show the origin of the false vasa recta. AA, interlobular arteries; Aa, transverse section of anastomotic arch; CV, cortical veins; *m*, glomeruli; R, R, false vasa recta; MV, medullary veins.

origin by the conveyance of minute venous radicles, so as to present a stellate appearance (*venæ stellulæ*). These vessels, which receive blood from the capsule of the kidney, pass inwards through the cortex and also join the venous arches.

With the exception of the blood brought by the false arteriæ rectæ

the blood supply of the medulla is to a great extent independent of that of the cortex, although of course the capillary network is continuous throughout. The pyramids are chiefly provided with blood by vessels which come off directly from the concave side of the arterial arches, and passing down into the boundary layer of the medulla there divide to form bunches or pencils of parallel or slightly diverging minute vessels (true arteriæ rectæ, fig. 572, *ar*), which by alternating with the bundles of uriniferous tubules which are passing up to the cortex to form the medullary rays, produce the characteristic streaked appearance of this part of the pyramid.

The long meshed capillary network which is supplied by the true arteriæ rectæ, is continued down to the apex of the papilla. Here the veins of the pyramid commence in a close plexus of small venous radicles surrounding the excretory ducts near their orifices (fig. 572, *vp*). Passing outwards towards the base of the pyramid, and receiving lateral branches at acute angles from its capillary network, the small veins become collected together into pencils, the vessels of which (venæ rectæ) are intermixed with the arteriæ rectæ, and unite into vessels which open into the concave side of the venous arch.

The venous trunks thence proceed, in company with the arteries, through the cortical septula between the pyramids, to the sinus of the kidney. Joining together, they escape from the hilus, and ultimately form a single vein, which lies in front of the artery, and ends in the inferior vena cava.

Lymphatics.—The lymphatics of the kidney are numerous, consisting of a superficial set forming a plexus in the fibrous capsule, and of deep lymphatics which issue from the hilus with the blood-vessels. Ludwig and Zawarykin have shown that there exists a network of freely intercommunicating lymphatic spaces between the tubules, in communication both with the lymphatics of the surface and those which issue with the blood-vessels at the hilus. They are most abundant in the cortical substance.

Nerves.—The nerves which have been traced into the kidneys are small. They come immediately from the renal plexus and the lesser splanchnic nerve, and contain filaments derived from both the sympathetic and cerebro-spinal systems. They may be traced accompanying the arteries as far as their finer branches, but it is uncertain how they end.

Intertubular Stroma.—Between the tubules and vessels of the kidney, although they are disposed closely together, a small amount of interstitial substance of the nature of connective tissue is found. It has a more fibrous character in the vicinity of the chief ramifications of the blood-vessels, and also around the Malpighian corpuscles, and the tubes of the medullary substance. The stroma is more abundant in the cortical substance, where it contains many connective tissue corpuscles, than in the greater part of the medullary substance; but it is very abundant towards the apices of the papillæ.

Literature.—*C. Ludwig*, Article "Kidney" in Stricker's Handbook, 1871 (where the literature up to that time will be found); *Eberth*, in Med. Centralbl., 1872; *Heidenhain*, in Arch. f. mikr. Anat., X. 1873; *W. Pye*, in Journ. of Anat. and Physiol., X. 1875; *Pansch*, in Arch. f. Anat., 1876 (position of kidney); *S. Schachowa*, Untersuch. ü. d. Nieren, Diss., Berne, 1876; *Drasch*, in Wiener Sitzungsb., 1877; *Langhans*, in Virch. Arch., 1878; *Budge*, in Deutsche med. Wochenschr., 1878; *Buchhammer*, in Arch. f. Anat., 1879 (varieties); *Cornil*, in Comptes rend., 1879; *Runeberg*, in Nord. med. ark., XI; *Henschen*, Akad. Afhandl. in Upsala, 1879.

THE URETERS.

The *ureters* are the two tubes which conduct the urine from the kidneys into the bladder. The dilated commencement of each, situated in the sinus of the kidney and into which the calices pour their contents, has already been described. Towards the lower part of the hilus of the kidney the pelvis becomes gradually contracted, and opposite the lower end of the gland, assuming the cylindrical form, receives the name of ureter.

The ureters measure from fourteen to sixteen inches in length; their ordinary width is about that of a goose-quill. They are frequently, however, dilated at intervals, especially near the lower end. The narrowest part of the tube, excepting its orifice, is that contained in the walls of the bladder.

Each ureter passes at first obliquely downwards and inwards, to enter the cavity of the true pelvis, and then curves forwards and inwards, to reach the base of the bladder. In its whole course, it lies close behind the peritoneum, and is connected to neighbouring parts by loose areolar tissue. Superiorly, it rests upon the psoas muscle, and is crossed very obliquely from within outwards, by the spermatic vessels, which descend in front of it. The right ureter is close to the inferior vena cava. Lower down, the ureter passes either over the common or the external iliac vessels, behind the termination of the ileum on the right side and the sigmoid flexure of the colon on the left. Descending into the pelvis, it enters the fold of peritoneum forming the corresponding posterior false ligament of the bladder, and, reaching the side of the bladder near the base (*u*, fig. 577), runs downwards and forwards in contact with it, below the obliterated hypogastric artery, and is crossed upon its inner side, in the male, by the vas deferens (*i*), which passes down between the ureter and the bladder. In the female, the ureters run along the sides of the cervix uteri and upper part of the vagina before reaching the bladder.

Having arrived at the base of the bladder, about two inches apart from one another, the ureters enter its coats, and running obliquely through them for about three-quarters of an inch, open at length upon the inner surface by two narrow and oblique slit-like openings, which are situated, in the male, about an inch and a half behind the urethral orifice, and about the same distance from each other. This oblique passage of the ureter through the vesical walls, while allowing the urine to flow into the bladder, has the effect of preventing its reflux.

Structure.—The walls of the ureter are pinkish or bluish white in colour. They consist of an external fibrous coat, a middle coat of plain muscular tissue, and a mucous lining. The muscular coat possesses two layers of longitudinal fibres and a middle circular layer.

The *mucous membrane*, thin and smooth, presents a few longitudinal folds when the ureter is laid open. It is composed of areolar tissue which becomes gradually loose towards the muscular coat, but there is no marked distinction into mucous and submucous layers. It is prolonged above to the papillæ of the kidney, and below becomes continuous with the lining membrane of the bladder. The epithelium (fig. 576) is of a peculiar character, like that of the bladder. It is stratified, consisting of at least three layers of cells, in the uppermost of which the cells are somewhat cubical, with depressions on their under surface, which

fit upon the rounded ends of a second layer of pear-shaped cells; then follow one or more layers of rounded or oval cells, with processes extending down to the mucous membrane.

Fig. 576.

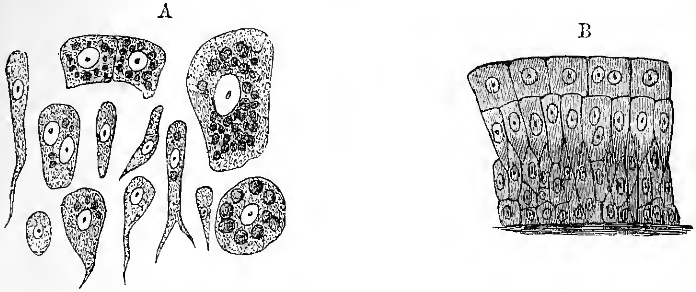


Fig. 576.—Epithelium from the pelvis of the human kidney (Kölliker.) 350 diameters.

A, different kinds of epithelial cells separated; B, the same in situ.

A few small mucous glands have occasionally been described at the upper end of the ureter and in the renal pelvis, but they appear not to be constantly present in man. Lymphoid nodules have also been met with in the pelvis of the kidney.

Vessels and Nerves.—The ureter is supplied with blood from small branches of the renal, the spermatic, the internal iliac, and the inferior vesical arteries. The veins end in various neighbouring vessels. The nerves come from the inferior mesenteric, spermatic, and hypogastric plexuses. They form plexuses in the outer and muscular coats containing a few ganglion-cells.

Varieties.—Sometimes there is no funnel-shaped expansion of the ureter at its upper end into a pelvis, but the calices unite into two or more narrow tubes, which afterwards coalesce to form the ureter. Occasionally, the separation of these two tubes continues lower down than usual, and even reaches as low as the bladder, in which case the ureter is double. In rare cases, a triple ureter has been met with.

In instances of long-continued obstruction to the passage of the urine, the ureters occasionally become enormously dilated.

THE URINARY BLADDER.

The *urinary bladder* (vesica urinaria) is a hollow receptacle for the urine, having an average capacity of about a pint when moderately distended, but capable of being distended to a considerably greater degree.

The average capacity of the bladder is often stated to be greater in the female than in the male; and, no doubt, instances of very large female bladders are not unfrequent, but these have probably been the result of unusual distension: in the natural condition, according to Luschka and Henle, the female bladder is decidedly smaller than that of the male.

The size and shape of the bladder, its position in the abdomino-pelvic cavity, and its relations to surrounding parts, vary greatly, according to its state of distension or collapse. When empty, the bladder lies deeply in the pelvis, and in a vertical antero-posterior section presents a triangular appearance, being flattened above and below, having

its base turned backwards and somewhat downwards, whilst its apex is directed forwards over the symphysis pubis. When moderately full, it is still contained within the pelvic cavity, and has a rounded form (fig. 577, *a*), but when completely distended, it rises above the brim of the pelvis, and becomes egg-shaped; its larger end, which is called the *base*, or *fundus*, being directed backwards towards the rectum in the male and the vagina in the female; and its smaller end, or *summit*,

Fig. 577.

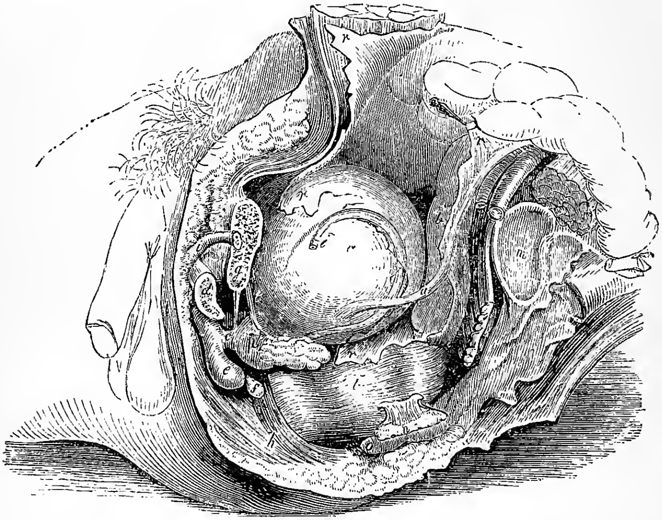


Fig. 577.—Lateral view of the viscera of the male pelvis (R. Quain). $\frac{1}{4}$

The left hip-bone has been disarticulated from the sacrum, the spinous process of the ischium cut through, and the pubis divided to the left of the symphysis; *a*, bladder; *b*, *b'*, rectum; *c*, membranous part of the urethra; *d*, section of the left corpus cavernosum; *e*, bulb of the spongy body of the urethra; *f*, Cowper's gland; *g*, section of the body of the pubis; *h*, sphincter ani muscle; *i*, part of the left vas deferens; *m*, articular surface of the sacrum; *n*, divided spine of the ischium; *o*, coccyx; *p*, prostate gland; *r*, *r*, peritoneum; *r'*, recto-vesical pouch; *u*, left ureter; *v*, left vesicula seminalis.

resting against the lower part of the anterior wall of the abdomen. Immediately in front of the base is the thickened portion often misnamed the *cervix*, or *neck*, from which the urethra abruptly leads off.

The long axis of the distended bladder is directed nearly horizontally from the base to the summit, in a line from the coccyx to a point somewhat above the symphysis pubis. In being gradually distended, the bladder curves slightly forwards, so that it becomes more convex behind than in front, and its upper end is by degrees turned more and more towards the front of the abdomen. Lastly, the bladder, when filled, appears slightly compressed from above downwards, so that its diameter in that direction is less than from side to side. In its ordinary state, the longest diameter in the male is from base to summit: but in the female its breadth is often greater than its height. During infancy the bladder is pyriform when distended, and lies chiefly in the abdomen.

Connections.—While freely moveable in all other directions upon surrounding parts, the bladder is fixed below to the walls of the pelvis by the neck, and by fibrous bands given off from the recto-vesical fascia (see Vol. I. p. 337), named the *true ligaments* of the bladder. It is supported, moreover, by strong areolar connections with the rectum or vagina, according to the sex, in a slighter degree by the two ureters, the obliterated hypogastric arteries and the urachus, by numerous blood-vessels, and, lastly, by a partial covering of the peritoneum, which, in being reflected from this organ in different directions, forms duplicatures, named the *false ligaments* of the bladder.

The *inferior* or *pubic surface* is entirely destitute of peritoneum, and is in apposition with the *recto-vesical fascia*, the symphysis and body of the pubis, and, if the organ be full, the lower part of the anterior wall of the abdomen. It is connected to these parts by loose areolar tissue, and to the back of the pubis by two strong bands of the recto-vesical fascia, named the *anterior true ligaments*. This surface of the bladder may be punctured above the pubis without wounding the peritoneum.

The *superior* or *abdominal surface* is entirely free, and covered everywhere by the peritoneum, which in the male is prolonged also for a short distance upon the base of the bladder. In the male, this surface is in contact with the rectum, and in the female with the uterus, as well as, in both sexes, with convolutions of the small intestine. Beneath the peritoneum, in the male, a part of the vas deferens is found on each side of the hinder portion of this surface.

The *summit* is connected to the anterior abdominal wall by a tapering median cord, named the *urachus*, which is composed of fibrous tissue, mixed at its base with plain muscular fibres which are prolonged upon it from the bladder. This cord, becoming narrower as it ascends, passes upwards from the apex of the bladder between the linea alba and the peritoneum, to reach the umbilicus, where it becomes blended with the dense fibrous tissue found in that situation.

The urachus, which forms in the early fœtal state a tubular communication between the urinary bladder and the allantoic vesicle, preserves, according to Luschka, vestiges of its original condition in the form of a long interrupted cavity, with irregularities and dilatations, lined with epithelium similar to that of the bladder, and sometimes communicating by a fine opening with the vesical cavity.

The *sides* of the bladder, when it is distended, are rounded and prominent, and are each of them crossed obliquely by the cord of the obliterated hypogastric artery, which is connected posteriorly with the superior vesical artery, and runs forwards and upwards to the umbilicus, approaching the urachus above the summit of the bladder. Behind and above this cord the side of the bladder is covered with peritoneum, but below and in front of it the peritoneum does not reach the bladder, which is here connected to the sides of the pelvic cavity by loose areolar tissue containing fat, and, near its anterior and lower part, by the broad expansion from the recto-vesical fascia, forming the *lateral true ligament*. The vas deferens crosses obliquely the hinder part of this lateral surface, from before backwards and downwards, and turning over the obliterated hypogastric artery, descends on the inner side of the ureter, along the back part of the superior surface, to the base of the bladder.

The *base* or *fundus* (fig. 578) is the widest part of the bladder. It is

directed downwards as well as backwards, and differs according to the sex in its relations to other parts. In the *male* it rests against the second portion of the rectum, and is covered superiorly for a short space by the peritoneum, which, however, is immediately reflected from it upon the rectum, so as to form the *recto-vesical pouch* (fig. 577, *r'*). Below the line of reflection of the serous membrane, the base of the

Fig. 578.

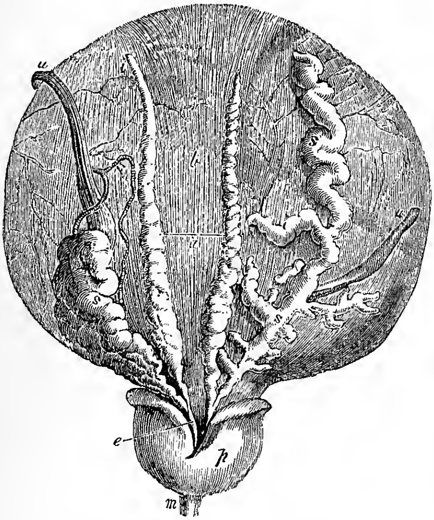


Fig. 578.—Base of the male bladder with the vesiculæ seminales, vasa deferentia, and prostate exposed (from Haller). $\frac{1}{2}$.

a, line of reflection of the peritoneum in the recto - vesical pouch ; *b*, the part above this from which the peritoneum has been removed, exposing the longitudinal muscular fibres ; *i*, left vas deferens ending in *e*, the left ejaculatory duct ; *s*, left vesicula seminalis joining the same duct ; the right vas deferens, and the right vesicula seminalis, marked *s*, *s*, unravelled, are also shown ; *p*, under side of the prostate gland, cut so as to exhibit the ejaculatory ducts ; *m*, small part of the membranous portion of the urethra ; *u*, *u*, the ureters, of which the right is turned to the side.

bladder is adherent to the rectum by dense areolar tissue over a triangular area bounded at the sides by the vasa deferentia and vesiculæ seminales (fig. 578 *s*, *s*), whilst its apex in front reaches the prostate gland (*p*). It is in this space, which in the natural state of the parts is by no means so large as it appears after they are disturbed in dissection, that the bladder may be punctured from the rectum without injury to the peritoneum. In the *female*, the base of the bladder is of less extent, and does not reach so far back in the pelvis as in the male : for it rests against the front of the neck of the uterus and the anterior wall of the vagina, both of which organs intervene between it and the rectum. This part of the bladder adheres to the vagina, and above that adhesion the peritoneum forms a pouch between it and the uterus, much shallower than the recto-vesical pouch of the male.

That part of the bladder where the urethra leads off from the cavity is the most strongly muscular part of the vesical wall, and in the male it is closely connected with the base of the prostate gland, by which it is supported. In both sexes this part of the bladder in the erect posture is lowest ; it lies at the angle of junction of the base and the pubic surface.

Ligaments of the bladder.—The *true ligaments* of the bladder, four in number, two anterior and two lateral, all derived from the vesical portion of the recto-vesical fascia, have been already noticed.

The *false ligaments* or *peritoneal folds* are described as five in number. Two of them, named *posterior* false ligaments or recto-vesical folds, run

forwards in the male along the sides of the rectum to the posterior and lateral aspect of the bladder, and bound the sides of the recto-vesical cul-de-sac. In the female these posterior folds pass forwards from the sides of the uterus, and are comparatively small. The two *lateral* false ligaments extend from the iliac fossæ to the sides of the bladder, each separated from the corresponding posterior ligament by a prominent angle in which the obliterated hypogastric artery lies. The *superior* false ligament (ligamentum suspensorium) is the portion of peritoneum between the ascending parts of the hypogastric arteries, and reaches from the summit of the bladder to the umbilicus.

Interior of the bladder.—On opening the bladder, its internal surface is found to be lined by a smooth membrane, which is comparatively loosely attached to the other coats, so that in the empty condition of the organ it is nearly everywhere thrown into small wrinkles or rugæ, which disappear as soon as the bladder is distended. Besides these, the interior of the bladder is often marked by reticular elevations or ridges, corresponding with fasciculi of the muscular coat.

At the lower part of the bladder is seen the orifice leading into the urethra, around which the mucous membrane is corrugated longitudinally. Immediately behind the urethral opening, at the lower part of the fundus, is a smooth triangular surface, having its apex turned forwards, which, owing to the firmer adhesion of the mucous membrane to the subjacent tissues, never presents any rugæ, even when the bladder is empty. This surface is named the *trigone* (trigonum vesicæ, Lieutaud) ; at its postero-superior angles are the orifices of the two ureters, situated about an inch and a half from each other, and nearly the same distance from the anterior angle, where the bladder opens into the urethra.

The orifices of the ureters, presenting the appearance of oval slits, are directed obliquely forwards and inwards : they are united by a curved elevation, convex forwards, which extends generally outwards and backwards beyond them, and which corresponds in position with a muscular band which joins them together and to the neck of the bladder. Proceeding forwards from opposite the middle of this, is another slight elevation of the mucous surface, named the *uvula vesicæ* which projects from below into the urethral orifice. In the female, the trigone is small, and the uvula indistinct. In the male the uvula lies a little in advance of the middle lobe of the prostate, and is sometimes prolonged on the floor of the prostatic portion of the urethra. It is produced by a thickening of the submucous tissue. In its natural state this may contribute to the more perfect closure of the orifice of the bladder ; when enlarged by disease it frequently produces considerable obstruction at the commencement of the urethra.

STRUCTURE OF THE BLADDER.

The bladder is composed of a *serous*, a *muscular*, a *submucous*, and a *mucous* coat, and supplied with numerous blood-vessels and nerves.

The **serous or peritoneal coat** is a partial covering, investing only the posterior and upper half of the bladder, and reflected from it upon the surrounding parts in the manner already described in detail.

The **muscular coat** consists of unstriped muscular fibres, so arranged as to warrant the usual description of them as forming layers, the outer

of which consists of bundles of fibres more or less longitudinal, and the next of fibres more circular in disposition ; while beneath this, is another imperfect longitudinal layer more recently recognised.

The *external* or *longitudinal fibres* (fig. 579, *a*, 580, *b*, and fig. 581, *a*, *b*,) are most distinctly marked on the anterior and posterior surfaces of the bladder. Commencing in front at the neck of the organ, from the pubes

Fig. 579.

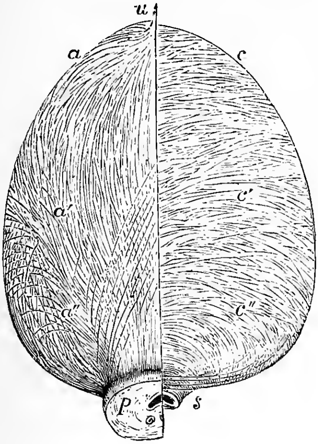


Fig. 580.

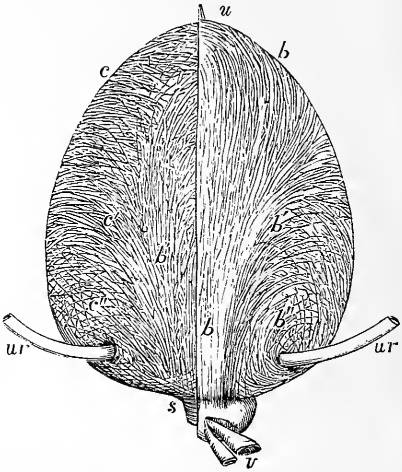


Fig. 579.—View of the muscular fibres of the bladder from before (Allen Thomson, after Pettigrew, and from nature). $\frac{1}{3}$

On the right side the superficial fibres are shown ; on the left the deep or circular fibres chiefly are displayed. *a*, on the right side, the median and most superficial bands of the longitudinal fibres, in which a slight decussation of fibres is seen ; *a'*, those diverging somewhat ; *a''*, the lowest, which pass much more obliquely ; the attachment of the longitudinal fibres to the prostate is shown ; on the left side, *c*, the upper, *c'*, the middle, *c''*, the lowest set of circular or deeper fibres ; at *s*, the thickest and most transverse sets of these fibres forming the sphincter ; *p*, half the prostate left on the right side, the left having been removed ; *u*, the urachus, into which some of the longitudinal fibres are seen prolonged.

Fig. 580.—View of the muscular fibres of the bladder from behind (Allen (Thomson, after Pettigrew, and from nature). $\frac{1}{3}$

On the right side the superficial fibres are displayed ; on the left the deeper fibres of the same kind or intermediate fibres, and some of the circular fibres ; *b*, *b*, the median, most superficial and strongest bands of longitudinal fibres on the right side ; *b'*, the more diverging set of fibres near the middle of the bladder ; *b''*, the most divergent fibres which surround the entrance of the ureters ; on the left side, *c*, *c'*, and *c''*, indicate the deeper circular fibres passing round at various levels and crossing with the deeper diverging fibres posteriorly ; *s*, the most transverse fibres at the neck forming the sphincter ; *u*, the urachus ; *ur*, the ureters ; the left half of the prostate has been removed to show the sphincter ; *v*, part of the right vas deferens and vesicula seminalis.

in both sexes (musculi pubo-vesicales), and, in the male, from the adjoining part of the prostate gland, they may be traced upwards along the anterior surface to the summit of the bladder ; and they may likewise be followed down over the posterior surface and base to the under part of the neck of the bladder, where they become attached to the prostate in the male, and to the front of the vagina in the female. Upon the sides

the superficial fasciculi run more or less obliquely, and often intersect one another: in the male they reach the prostate. At the summit a few are continued along the urachus. The longitudinal fibres taken together, constitute what has been named the *detrusor urinæ* muscle.

The so-called *circular* fibres form a thin and somewhat irregular reticulated layer distributed over the body of the bladder, having various appearances in different bladders. Their course may in general be looked upon as transverse, but for the most part throughout the upper two-thirds of the bladder they cross one another in very oblique bands: towards the lower part of the organ they assume a more circular course, and upon the fundus and trigone form a tolerably regular layer. Close to and around the cervix, in immediate connection with the prostate in the male, they densely encircle the orifice and constitute what has been named the *sphincter vesicæ*, which, however, is not distinct from the other fibres, and according to Henle does not perform the function of a sphincter but can only serve to complete the evacuation of this part of the bladder, the part of a sphincter being performed by the muscular tissue of the prostate.

The *third stratum* of fibres, still more deeply situated, and which might be termed internal longitudinal, was first described by Ellis, who distinguished it as "submucous." It is thin, and its bundles have a reticular arrangement but with a general longitudinal direction.

Fig. 581.

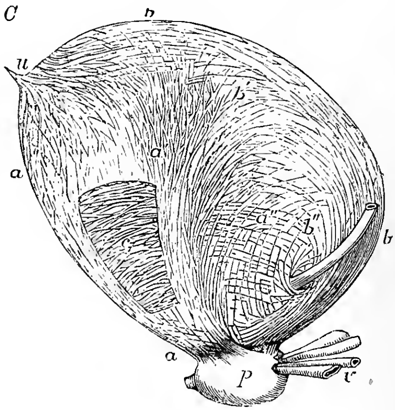


Fig. 581.—View of the muscular fibres of the bladder from the left side (Allen Thomson, after Pettigrew, and from nature). $\frac{1}{3}$

The anterior and posterior superficial fibres are seen running from below upwards, crossing each other by their divergence on the side of the bladder, and are indicated by the same letters as in the preceding figures; at *c*, a portion of the anterior longitudinal fibres has been removed so as to expose the deeper circular fibres.

The muscular coat of the bladder forms so irregular a covering, that, when the organ is much distended, intervals arise in which the walls are very thin; and, should the internal or mucous lining protrude in any spot through the muscular bundles, a sort of hernia is produced, which may go on increasing, so as to form what is called a vesical sacculus, or *appendix vesicæ*, the bladder thus affected being termed *sacculated*. Hypertrophy of the muscular fasciculi, which is liable to occur in stricture of the urethra or other affections impeding the issue of the urine, gives rise to that condition named the *fasciculated* bladder, in which the interior of the organ is marked by strong reticulated ridges or columns, with intervening depressions.

Next to the muscular coat, between it and the mucous membrane, but much more intimately connected with the latter, is a well-marked layer of areolar tissue, the vascular or **submucous coat**. This submucous

areolar layer contains a large number of fine coiled fibres of elastic tissue.

The **mucous membrane** of the bladder is soft, smooth, and of a pale rose colour. It is continuous above with the lining membrane of the ureters and kidneys, and below with that of the urethra. Neither here nor in the ureters is the mucous membrane provided with a muscularis mucosæ. It adheres loosely to the muscular tissue, and is thus liable to be thrown into wrinkles, except at the trigone, where it is always more even. It is covered with a stratified epithelium, similar to that of the ureters. The cells vary much in form according to the condition of distension of the bladder, for in the distended organ they are flattened out so as to cover a larger surface, while in the empty condition of the bladder they are of less diameter and proportionately higher.

Vessels.—The *superior vesical arteries* proceed from the remaining pervious portions of the hypogastric arteries; in the adult they appear as direct branches of the internal iliac. The *inferior* vesical arteries are usually derived from the anterior division of the internal iliac. In the female the uterine arteries also send branches to the bladder. The neck and base of the organ appear to be the most vascular portions. The *veins* form large plexuses around the neck, sides, and base of the bladder; they eventually pass into the internal iliac veins. The *lymphatics* follow a similar course.

The **nerves** are derived partly from the hypogastric plexus of the sympathetic, and partly from the sacral plexus of the cerebro-spinal system. The former are said to be chiefly distributed to the upper part of the bladder, whilst the spinal nerves may be traced more directly to its neck and base. According to Kisselew, the nerves form a network immediately under the epithelium, from which filaments pass amongst the epithelium cells, where they end in special cells. Gangliated plexuses of nerves accompany the blood-vessels, and send branches both to these and to the muscular coat of the bladder (F. Darwin).

Recent literature of the bladder and ureters.—*Obersteiner* in Sticker's Handbook, 1871; *Daneffe u. v. Welter*, (portion of bladder) Mém-pres. à l'acad. roy. de méd., Bruxelles, 1872; *Jurié* in Wiener med. Jahrb. IV. 1873; *Egli* in Arch. f. mikr. Anat., IX. (glands in pelvis); *Paneth* in Wiener Sitzungsb., 74, 1876 (epithelium); *Weigert*, *Hofmann* in Virch. Arch. LXX., LXXII., 1877 (abnormalities of ureter); *Hofmann*, ibid. (capacity of bladder); *Hamburger*, in Arch. f. mikr. Anat., XVII; *Mayer*, in Virch. Arch. LXXXV. (ganglion-cells in ureter).

On the muscular arrangements of the bladder, see Ellis, in Trans. Med. Chir. Society, 1856, and Demonstrations of Anatomy; Pettigrew, in Phil. Trans. for 1866; Sabatier, Rech. anat. et phys. sur les appareils musculaires correspondants à la vessie et à la prostate dans les deux sexes, 1864; *Cadiat* in Gaz. méd. V., 1876 (sphincter vesicæ).

REPRODUCTIVE ORGANS.

I. IN THE MALE SEX.

Under this head are included—1, the testes with their ducts and coverings; and, 2, the urethra, with certain accessory parts, such as the prostate and Cowper's glands. The urethra in the male is at once the outlet for the urine from the bladder and the products of secretion from the sexual glands. Extending from the neck of the bladder to the extremity of the penis, it is surrounded in its first part by the prostate gland, and there receives the excretory ducts of the testes and vesiculæ seminales; its second part passes through the triangular ligament of the perineum; and its third and longest part passes along the perineum and penis, surrounded by the corpus spongiosum.

THE PROSTATE GLAND.

The *prostate gland* is a firm, glandular, and muscular body, somewhat resembling a chestnut in shape and size, which adjoins the neck of the bladder, and encloses the first part of the urethra: it is placed in the pelvic cavity, on the upper aspect of the subpubic fascia, and rests posteriorly against the rectum. Its posterior or rectal surface is larger than its flattened anterior or pubic surface. It usually measures about an inch and a half across at its widest part, an inch and a quarter from its base to its apex, and nearly an inch in thickness. Its ordinary weight is about six drachms.

The pubic surface of the prostate is flattened and marked with a slight longitudinal furrow; it is about half an inch or rather more from the pubic symphysis, and there, as well as at the sides, the gland is con-

Fig. 582.

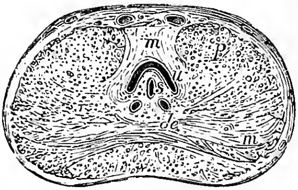


Fig. 582.—Transverse section of the prostate gland through the middle. (Allen Thomson.)

u, the urethra into which the eminence of the caput gallinaginis rises from below; *s*, the sinus or utricle cut through; *d e*, the ejaculatory ducts; *m*, superiorly, the deep sphincter muscular fibres; *m*, lower down, intersecting muscular bands in the lateral lobes of the prostate; *p*, glandular substance.

nected to the pubic bones by the thickenings of the pelvic fascia, which form the pubo-prostatic ligaments or anterior ligaments of the bladder. The posterior or rectal surface is smooth, and is marked by a slight depression, or by two grooves, which meet in front, and correspond with the course of the seminal ducts, as well as mark the limits of the lateral lobes in this situation: it is in close apposition with the rectum, immediately in front of the bend from the middle to the lower or anal part of that viscus, where the surface and superior border of the gland can be felt by the finger introduced into the intestine. The sides are convex and prominent, and are covered by the anterior portion of the levatores ani muscles, which pass back on each side, from the pubis and triangular ligament of the urethra, and embrace the sides of the prostate. The base of the gland directed towards the bladder is of considerable thickness, and is notched in the middle: its apex is turned towards the triangular ligament. As already stated, the prostate encloses the first part of the urethra. The canal runs nearer to the anterior than to the posterior surface of the gland, so that in general it is about a quarter of an inch distant from the former and about one-third of an inch from the latter; but it frequently varies greatly in this respect. The prostatic portion of the urethra is about an inch and a quarter long, and is dilated in the middle; it contains the colliculus seminalis and the openings of the seminal and prostatic ducts, as will be afterwards more particularly described. The common or ejaculatory seminal ducts, which pass forwards from the vesiculæ seminales, also traverse the lower part of the prostate, enclosed in a special hollow part of the gland, and open into the urethra; and in the middle, close in front of these, is the prostatic utricle.

The prostate is usually described as consisting of three lobes, two of

which, placed laterally, and meeting behind in the posterior notch, and continuous in front of the urethra, are of equal size ; the third or middle lobe, is a smaller mass, intimately connected with the other two, and fitting in between them and the bladder and adjacent part of the urethra. When prominent it corresponds to the elevation in the urinary bladder called the uvula. The separation between the lobes of the prostate, which is normally little marked, becomes often abnormally much more apparent.

Structure.—The prostate gland is covered externally by a dense fibrous coat, which is continuous with the recto-vesical fascia, and with the superior layer of the triangular ligament. This fibrous capsule is divisible into two layers, between which the prostatic plexus of veins is enclosed (Adams). The glandular substance is associated with a large quantity of plain muscular tissue, which forms the principal part of the stroma of the organ. This muscular tissue forms an external layer below the fibrous capsule, and extends everywhere through the glandular substance : there is also a strong layer of circular fibres continuous posteriorly with the sphincter vesicæ, and in front with the thin layer surrounding the membranous part of the urethra. The part of the prostate in front of the urethra is almost entirely muscular ; in the hinder part the muscular substance is in greatest quantity near the bladder.

The *glandular substance* is spongy and yielding ; its colour is reddish grey, or sometimes of a brownish hue. It consists of numerous tubular alveoli, which unite into a smaller number of excretory ducts. The epithelium is columnar throughout. According to Langerhans there is a second layer of small cells next the basement membrane between the tapered ends of the columnar cells. In the upper part of the gland the acini are smaller and more saccular ; in the middle and lower parts the tubes are longer and convoluted at their ends. The capillary blood-vessels form a close network as in other similar glands on the ducts and acini, and the different portions of the gland are united by areolar tissue, and supported by processes of the deep layer of the fibrous capsule and by the muscular stroma. The ducts open by from twelve to twenty or more orifices upon the floor of the urethra, chiefly in the hollow on each side of the colliculus seminalis.

As age advances, this gland often becomes enlarged and its ducts may contain small round albumino-calcareous concretions of laminated appearance, and varying in size up to that of a millet seed.

Vessels and Nerves.—The prostate is supplied by branches of the vesical, hæmorrhoidal, and pudic *arteries*. Its *veins* form a plexus embedded in the fibrous covering round the sides and base of the gland, which is highly developed in old subjects. These veins communicate in front with the dorsal vein of the penis, and behind with branches of the internal iliac vein. Lymphatics ramify with the veins, between the two layers of the fibrous capsule. The *nerves*, which are derived from the hypogastric plexus, consist of both medullated and non-medullated fibres, and are interspersed with ganglion cells. Pacinian bodies have also been observed on the superficial nerves.

Secretion.—Examined after death, the *prostatic fluid* has a milky aspect, due to the admixture of a large number of epithelial cells, but probably, during life, it is more transparent. According to Adams, the fluid has an acid reaction, and presents, under the microscope, numerous granules, epithelial cells and nuclei. Some of the granules are composed of lecithin (Fürbringer, in Jena Sitzungsb., 1881).

THE PENIS.

The **penis** is composed principally of erectile tissue, arranged in three long somewhat cylindrical masses, which are enclosed in fibrous sheaths, and are united together so as to form a three-sided prism which receives a covering from the general integument. Of these masses, two, named *corpora cavernosa penis*, placed side by side, form the principal part of the organ, whilst the other, situated beneath the two preceding, surrounds the canal of the urethra, and is named *corpus cavernosum urethræ* or *corpus spongiosum*.

The penis is attached at its root to the symphysis of the pubes, and to the pubic arch; in front it ends in an enlargement named the *glans*, which is structurally similar to and continuous with the corpus spongiosum. The intermediate portion or *body* of the penis, owing to the manner in which its three component parts are united together, has three somewhat flattened sides and three rounded borders: the upper side is named the *dorsum*. The *glans* penis, which is slightly compressed above and below, has at its extremity a vertical fissure forming the external orifice of the urethra; its base, which is wider than the body of the penis, is hollowed out to receive the narrowing extremities of the corpora cavernosa; its border is rounded and projecting, and is named the *corona glandis*, behind which is a constriction of the penis named the *cervix*. The median fold of integument connecting the glans below the urethral orifice to the inferior border of the penis is named the *frænum* of the prepuce.

The integument of the penis, which is continued from that of the pubes and scrotum, forms a simple investment as far as the neck of the glans. Here it is doubled up in a loose fold, the *prepuce* or *fore-skin*. The inner layer of this fold is firmly attached behind the cervix; and from thence the integument, becoming closely adherent, is continued forwards over the corona and glans, as far as the orifice of the urethra, where it meets with the mucous membrane of the urethra. Upon the body of the penis the skin is thin, free from fat, and, in the anterior two-thirds of its length, from hairs also; in these respects differing remarkably from that on the pubes, which is thick, covers a large cushion of fat, and, after puberty, is beset with hairs: the skin of the penis is moreover very movable and distensible, and is of a darker colour than that of the neighbouring parts. At the free margin of the prepuce the integument changes its character, and approaches that of a mucous membrane, being red, thin, and moist. Numerous sebaceous glands are collected round the cervix of the penis and corona glandis; they are named the *glands of Tyson*, or glandulæ odoriferæ, their secretion having a peculiar odour.

Upon the surface of the glans the integument again changes its character; it contains no glands, but is beset with large vascular and nervous papillæ, and it adheres most intimately and immovably to the spongy tissue of the glans.

Beneath the skin, on the body of the penis, the ordinary superficial fascia is very distinct; it is continuous with that of the groin, and also with the dartos tissue of the scrotum. Near the root of the organ there is in front a dense band of fibro-elastic tissue, named the *suspensory ligament*, lying amongst the fibres of the superficial fascia; it is triangular in form; its anterior border is free, above it is connected with the fore

part of the pubic symphysis, and below it runs down upon the dorsum of the penis.

The integuments of the penis are supplied with blood by branches of the dorsal artery of the penis and external pudic; the veins join the dorsal and external pudic veins. Their nerves are derived from the dorsal and anterior superficial perineal branches of the pudic nerves.

THE CORPORA CAVERNOSA.

The **corpora cavernosa** form the principal part of the body of the penis, and chiefly determine its form and consistence in the state of erection. They are two cylindrical bodies, placed side by side, flattened on their median aspects, and closely united and in part blended together along the middle line in the anterior three-fourths of their length; whilst at the back part, in contact with the symphysis pubis, they separate from each other in the form of two bulging and then tapering processes named *crura*, which, extending backwards, are attached to the pubic and ischial rami, and are invested by the erectores penis or ischio-cavernosi muscles. The enlarged portion at the root, named by Kobelt the *bulb of the corpora cavernosa*, attains a much greater proportionate development in some quadrupeds than in man. In front, the corpora cavernosa are closely bound together into a blunt conical extremity, which is covered by the glans penis and firmly connected to its base by fibrous tissue.

Fig. 583.

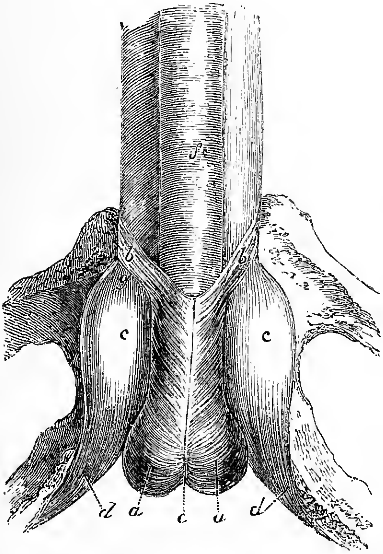


Fig. 583.—Root of the penis attached to the rami of the pubes and ischium (from Kobelt). $\frac{2}{3}$

a, a, accelerator urinæ muscle covering the bulb of the spongy body of the urethra, which presents at *e*, posteriorly, a median notch; *b, b*, anterior slips of the muscle or bulbo-cavernosi; *c, c*, crura of the penis, presenting an oval dilatation or bulb of the corpus cavernosum; *d, d*, erectores penis muscles; *f*, corpus spongiosum urethræ.

The under surface of the united cavernous bodies presents a longitudinal groove, in which is lodged the corpus spongiosum. The upper or anterior surface is also marked with a slight median groove in which the dorsal vein of the penis is situated, and near the root is attached to the pubes by the suspensory ligament.

Structure.—The median septum between the two corpora cavernosa is thick and complete near the root of the penis; but farther forward it becomes thinner, and only imperfectly separates their cavities, for it exhibits, particularly towards the anterior extremity, numerous clefts, extending from the dorsal to the urethral edge, and admitting of a free communication between the erectile tissue of the two sides. From the direction of these slits, the intermediate white portions of the septum

resemble somewhat the teeth of a comb, and hence the partition has received the name of *septum pectiniforme.*

The external fibrous investment of the cavernous structure is white and dense, from $\frac{1}{24}$th to $\frac{1}{12}$th of an inch thick, and very strong and elastic. It is composed for the most part of longitudinal bundles of shining white fibres, with numerous well-developed elastic fibres, enclosing the two corpora cavernosa in a common covering; and internal to this, each corpus cavernosum is surrounded by a layer of circular fibres, which enter into the formation of the septum.

Fig. 584.

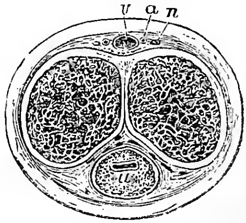


Fig. 584.—Transverse section of the penis in the distended state (altered from Henle).

The outer outline indicates the integument surrounding the deeper parts; the erectile tissues of the corpora cavernosa and the septum pectiniforme are shown in section; *u*, placed on the section of the spongy body, below the urethra; *v*, the single dorsal vein; *a*, the dorsal artery, and *n*, the nerve of one side.

From the interior of the fibrous envelope, and from the sides of the septum, numerous lamellæ, bands, and cords, composed of fibrous elastic and plain muscular tissue, and named *trabeculæ*, pass inwards, and run through and across the cavity in all directions, thus subdividing it into a multitude of interstices, and giving the entire structure a spongy character.

The trabeculæ, whether lamelliform or cord-like, are larger and stronger near the circumference than along the centre of each cavernous body, and they also become gradually thicker towards the crura. The interspaces, conversely, are larger in the middle than near the surface; their long diameter is, in the latter situation, placed transversely to that of the penis: and they become larger towards the forepart of the penis. They are occupied by venous blood, being in reality large cavernous veins, and are lined by a layer of flattened epithelium similar to that lining other veins.

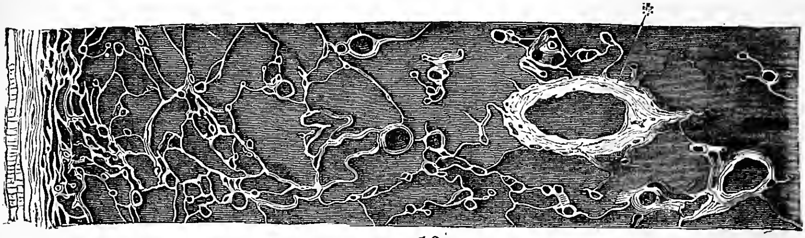
Fig. 585.

Fig. 585.—Portion of the erectile tissue of the corpus cavernosum magnified, showing the areolar structure and the vascular Distribution (from J. Müller).

a, a small artery supported by the larger trabeculæ, and branching out on all sides; *c*, the tendril-like arterial tufts or helicine arteries of Müller; *d*, the areolar structure formed by the finer trabeculæ.

The intertrabecular spaces thus form a labyrinth of intercommunicating venous areolæ divided by the trabecular tissue, and opening freely from one corpus cavernosum to the other through the septum, especially in front. The blood is carried away from these spaces by two sets of veins, the one set joining the prostatic plexus and pudendal veins ; the others passing into the dorsal vein. Of these last some issue

Fig. 586.



$\frac{10}{1}$

Fig. 586.—Part of a section of one of the corpora cavernosa, injected from the deep artery of the penis (Henle).

On the left is seen the fibrous tissue ; at *, a section of the arteria profunda penis.

from between the corpus cavernosum and the spongy body of the urethra, encircling the penis nearly at right angles, while others pass more directly into the dorsal vein from the upper surface.

The principal arteries of the corpora cavernosa are the cavernous

Fig. 587.

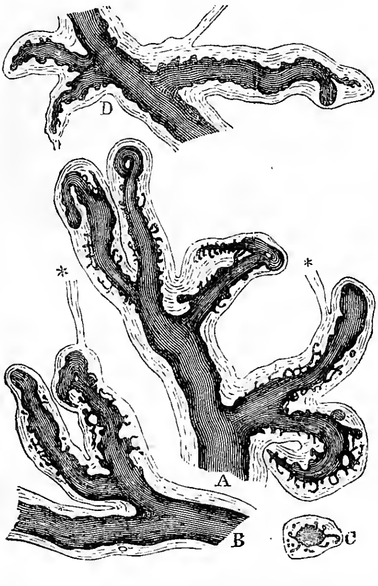


Fig. 587.—Helicine arteries with their sheaths, &c. (from Henle). Magnified with a low power.

A and B, from the corpus cavernosum penis ; D, from the corpus spongiosum urethræ ; C, transverse section of one of the helicine arteries ; in this and the other figures the smaller lateral prolongations of the arterial vessels into the sheath are shown ; * *, fasciculi of connective tissue passing off from the summit of two of the sheaths.

branches of the pudic arteries (profundæ penis), of the right and left sides ; but the dorsal artery of the penis also sends small twigs through the fibrous sheath of the corpora cavernosa, along the upper surface, especially in the fore part of the penis. Within the cavernous tissue, the numerous branches of arteries are supported by the trabeculæ, in the middle of which they run, and terminate in branches of capillary minuteness which open into the intertrabecular spaces ; some of the arterial twigs projecting into the spaces, and forming peculiar

curling and somewhat dilated vessels, which were named by J. Muller, *helicine* arteries. These are usually bound down by small fibrous bands (fig. 587,* *), and it appears to be due to this circumstance that these projecting vessels acquire a looped or tortuous aspect when distended with injection.

The helicine arteries are most abundant in the posterior part of the corpora cavernosa, and are found in the corresponding part of the corpus spongiosum also; but they have not been seen in the glans penis. They are more distinct in the human subject than in animals, where they are often missed. Small capillary branches pass from them to supply the tissue of the enclosing sheath.

In addition to the blood which passes into the venous spaces from the capillary network of the sheath and trabeculæ some small arteries are said by C. Langer to open directly into the larger venous spaces.

CORPUS SPONGIOSUM.

The **corpus spongiosum urethræ** commences in front of the triangular ligament of the perineum, where it is placed between the diverging crura of the corpora cavernosa, and somewhat behind their point of junction. The enlarged and rounded posterior extremity is named the *bulb*, and is situated below the urethra. It extends forwards as a cylindrical, or slightly tapering body, lodged in the groove on the under side of the united cavernous bodies, as far as their blunt conical anterior extremity, over which it expands so as to form the glans penis already described. In the whole of this extent it encloses the urethra.

Fig. 588.

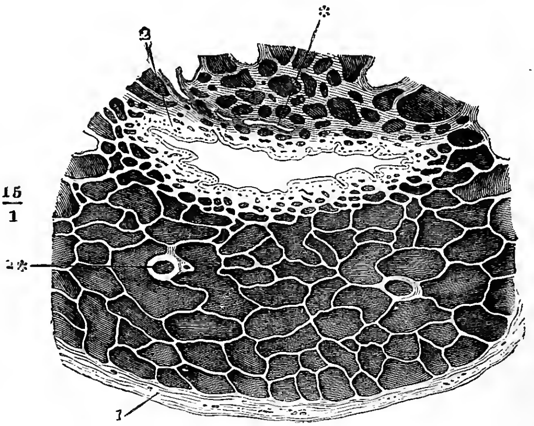


Fig. 588.—SECTION OF THE CORPUS SPONGIOSUM INJECTED FROM ITS ARTERY (Henle).

1, fibrous tunic of the corpus cavernosum; 2, mucous membrane of the urethra. * Section of a lacuna of the mucous membrane; * * section of an artery.

The posterior bulbous part, or *bulb of the urethra*, varies in size in different subjects. It receives an investment from the triangular ligament on which it rests, and is embraced by the accelerator urinæ, or bulbo-cavernosus muscle. The posterior extremity of the bulb exhibits, more or less distinctly, a subdivision into two lateral portions or lobes, separated by a slight furrow on the lower surface, and by a slender fibrous partition within, which extends for a short distance forwards; in early infancy this is more marked. It is above this part that the urethra, having pierced the triangular ligament, enters the bulb, surrounded obliquely by a portion of the spongy tissue, named by Kobelt the *colliculus bulbi*, from which a layer of venous erectile tissue passes back upon the membranous and prostatic portions of the urethra to the

neck of the bladder, lying closely beneath the mucous membrane. At first the urethra is nearer the upper than the lower part of the corpus spongiosum, but it soon gains and continues to occupy the middle of that body.

Structure.—This is essentially the same as that of the corpora cavernosa, but with a much less developed fibrous framework. Like the corpora cavernosa, it is distended with blood during erection, but it never acquires the same rigidity. The fibrous tunic (fig. 588, 1) is much thinner, is less white in colour, and contains more elastic tissue; the trabeculæ are finer and more equal in size; the areolæ are smaller, more uniform, and directed for the most part with their long diameter in the line of that of the penis; in the glans, the meshes are smallest and most uniform. Plain muscular fibres immediately surround the canal of the urethra, and also form part of the external coat of the spongy substance. A considerable artery derived from the internal pudic enters the bulb on each side, and supplies the greater part of the spongy body, sending branches as far as the glans penis, but this part is chiefly supplied by branches from the arteria dorsalis. Besides these, there is another but much smaller branch of the pudic artery, entering the bulb on the upper surface, about an inch from its posterior extremity, and running forwards in the corpus spongiosum to the glans (Kobelt). The arteries open into the venous spaces chiefly if not entirely by the intervention of capillaries. Veins issue from the glans and adjoining part of the spongy body, to end in the vena dorsalis penis; those of the rest of the spongy body for the most part pass backwards through the bulb, and end in the prostatic and pudic venous plexuses: some emerge from beneath the corpora cavernosa, anastomose with their veins, and end partly in the cutaneous veins of the penis and scrotum, and partly in the pudic and obturator veins.

The **lymphatics** of the penis form a dense network on the skin of the glans and prepuce, and also underneath the mucous lining of the urethra. They pass chiefly into the inguinal glands. Deep-seated lymphatics are also described as issuing from the cavernous and spongy bodies, and passing under the pubic arch with the deep veins, to join the lymphatic plexuses in the pelvis.

The **nerves** of the penis are derived from the dorsal and superficial perineal branches of the *pudic nerve* and from the *hypogastric plexus* of the sympathetic. The former are distributed to the skin and mucous membrane, the latter entirely to the cavernous and spongy bodies. Simple and compound end-bulbs occur numerously on the nerves of the penis, and Pacinian bodies have been found on the nerves of the glans.

URETHRA OF THE MALE.

The **male urethra** extends from the neck of the bladder to the extremity of the penis. Its total length is about eight inches and a half, but varies much according to the length of the penis, and the condition of that organ. Except during the passage of urine or semen the canal is a mere cleft elongated transversely and with the superior and inferior parts of the wall in contact (see fig. 584, *u*). Its diameter when moderately distended varies at different parts of its extent, as will be stated more particularly hereafter. The tube consists of a continuous mucous membrane, supported by an outer layer of submucous tissue connecting it with the several parts through which it passes. In the submucous tissue there are, throughout the whole extent of the urethra, two layers

of plain muscular fibres, the inner fibres disposed longitudinally, and the outer in a circular direction. The urethra is described under the three divisions of the *prostatic*, *membranous*, and *spongy* portions.

Fig. 589.

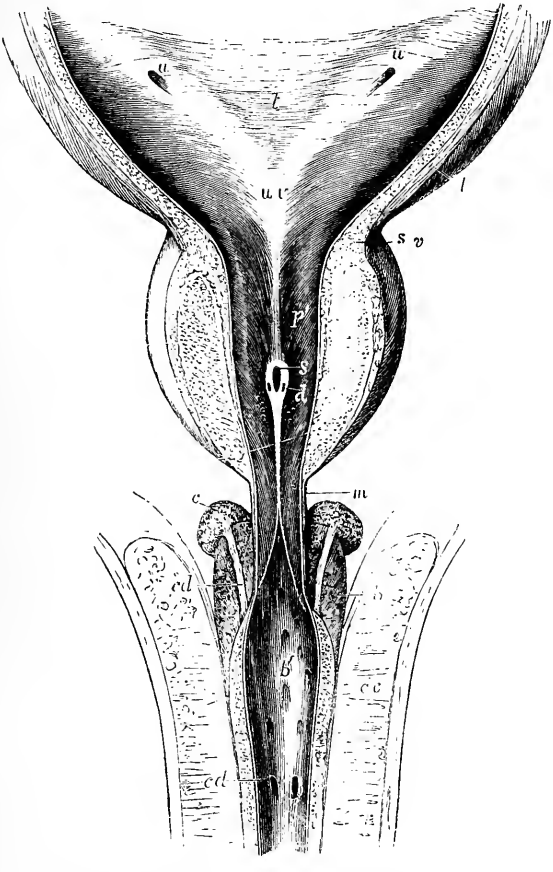


Fig. 589.—The lower part of the bladder and the prostatic, membranous, and bulbous parts of the urethra opened from above. (Allen Thomson.)

A portion of the wall of the bladder and the upper part of the prostate gland have been removed, the corpora cavernosa penis have been separated in the middle line and turned to the side, and the urethra has been slit up ; the bulb is left entire below, and upon and behind it the glands of Cowper with their ducts have been exposed. *t*, placed in the middle of the trigonum vesicæ ; *u*, *u*, oblique apertures of the ureters ; from these an elevation of the wall of the bladder is shown running down to *u v*, the uvula vesicæ ; *l*, the longitudinal muscular fibres of the bladder passing down upon the prostate ; *s v*, the circular fibres of the sphincter ; *p*, the glandular part of the prostate ; *p′*, the prostatic portion of the urethra ; from the uvula vesicæ a median ridge is seen descending to the caput gallinaginis, in which *s* indicates the opening of the prostatic utricle, and *d*, that of one of the ejaculatory ducts ; *m*, the commencement of the membranous portion of the urethra ; *b*, the bulb of the spongy body ; *b′*, the bulbous part of the urethra ; *c*, one of Cowper's glands ; *c d*, *c d*, course and orifice of its duct lying upon the bulb, and passing forward between the spongy body and the urethra, into which along with its fellow it opens ; *c c*, one of the corpora cavernosa.

1. The first, or **prostatic portion,** is the part which passes through the prostate gland. It is about 1¼ inches in length, is the widest part of the canal, and is wider in the middle than at either end : at the neck of the bladder its diameter is nearly one-third of an inch, in the next part it widens a little, so as to be rather more than this (in old persons nearly half an inch), farther on it diminishes, until, at its anterior limit, it is smaller than at its commencement. It passes through the upper part of the prostate, above the middle lobe. Though enclosed in the firm glandular substance, it is more dilatable than any other part of the urethra ; but immediately at the neck of the bladder, it is much more resistant. The transverse section of the urethra, as it lies in the prostate, is slightly curved with the convexity upwards.

The lining membrane of the prostatic portion of the urethra is thrown into longitudinal folds, when not distended by fluid. Towards the neck of the bladder, a slight elevation on the lower surface passes back into the uvula vesicæ. Somewhat in advance of this, and continued from it along the floor of the passage, projects a narrow median ridge, about three quarters of an inch in length, and one eighth of an inch in its greatest height ; this ridge gradually rises into a peak, and sinks down again at its anterior or lower end, and is formed by an elevation of the mucous membrane and subjacent tissue. This is the crest of the urethra (crista urethræ), which also receives the names of *colliculus seminalis*, *caput gallinaginis* and *verumontanum*. On each side of this ridge the surface is slightly depressed, so as to form a longitudinal groove, named the *prostatic sinus*, the floor of which is pierced by numerous foramina, the orifices of the prostatic ducts. Through these a viscid fluid oozes out on pressure ; the ducts of the middle lobe open behind the urethral crest, and some others open before it. The prostatic urethral mucous membrane is covered by a laminated epithelium like that of the bladder.

At the fore part of the most elevated portion of the crest, and exactly in the middle line, is a recess, upon or within the margins of which are placed the slit-like openings of the common seminal or ejaculatory ducts, one at each side. This median depression leads into the prostatic vesicle, which has been named also *sinus pocularis*, *utricle* or *uterus masculinus*. It was first described by Morgagni, and corresponds with the uterus in the female.

The vesicle forms a cul-de-sac running upwards or backwards, from three to five lines deep, and usually about one quarter to nearly half an inch wide at its entrance and for some distance up, but acquiring a width of at least one twelfth of an inch at its further end or fundus. The narrow portion runs in the urethral crest, and its fundus lies behind and beneath the middle lobe, and between the two lateral lobes of the prostate. Its parietes, which are distinct, and of some thickness, are composed of fibrous tissue and mucous membrane, together with a few muscular fibres, and enclose on each side the ejaculatory duct ; numerous small ramified and convoluted glands open on its inner surface. The epithelial lining is of the laminated kind. The caput gallinaginis contains some well-marked erectile and plain muscular tissue, and it has been supposed that this eminence, when distended with blood, may offer an obstacle to the passage of the semen backwards into the bladder.

2. The **membranous portion** of the urethra comprises the part between the apex of the prostate and the bulb of the corpus spongiosum. It is three quarters of an inch long, but about half an inch of its posterior

surface is covered by the bulb of the corpus cavernosum which projects backwards over it. This membranous portion is the narrowest division of the urethra. In the middle its diameter is one-fifth of an inch : at the end not quite so much. It is placed beneath the pubic arch, the anterior concave surface being distant nearly an inch from the bone, leaving an interval, occupied by the dorsal vessels and nerves of the penis, by areolar tissue, and some muscular fibres. Its lower convex surface is turned towards the perinæum, opposite the point of meeting

Fig. 590.

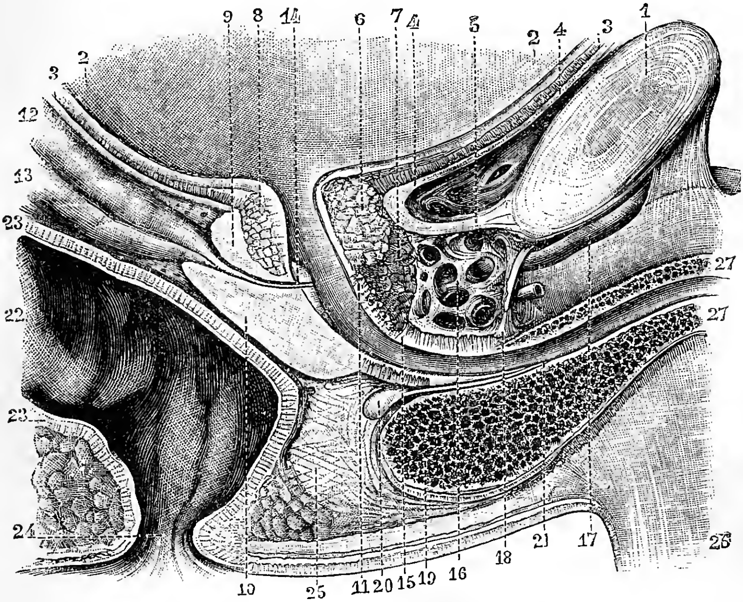


Fig. 590.—Sagittal section of the commencement of the urethra passing a little to the left of the middle line (Sappey).

1, Symphysis pubis ;- 2, bladder ; 3, 4, section of its wall ; 5, pubo-prostatic ligament; 6 to 11, different parts of the prostate ; 12, left vas deferens ; 13, left seminal vesicle ; 14, ejaculatory duct, opening on the veru montanum ; 15, wall of the membranous part of the urethra ; 16, areolar tissue with venous plexus, into which the vena dorsalis penis, 17, is seen passing : 18, triangular ligament ; 19, bulb of the corpus spongiosum ; 20, Cowper's gland ; 21, its duct ; 22, cavity of the rectum ; 23, its walls ; 24, anus ; 25, areolar and muscular tissue lying between the rectum and bulb ; 26, septum scroti ; 27, corpus spongiosum urethræ.

of the transverse muscles ; it is separated by an interval from the last part of the rectum. About $\frac{1}{12}$th of an inch in front of the prostate it emerges from between the anterior borders of the levatores ani, and passes through the deep layer of the subpubic fascia ; it then lies between that and the anterior layer (triangular ligament) through which it passes someway farther forwards. Both these fibrous membranes are prolonged upon it, the one backwards and the other forwards. Between these two layers the urethra is surrounded by erectile tissue, by some veins, and also by plain muscular tissue, whilst the fibres of the *compressor urethræ* muscle are beneath it. On each side are Cowper's glands.

The plain muscular fibres of this portion of the urethra are continued over the outer and inner surfaces of the prostate into the muscular fibres of the bladder posteriorly, and into those of the spongy portion of the urethra anteriorly (Hancock).

3. The **spongy portion** of the urethra, by far the longest and most variable in length and direction, includes the remainder of the canal, or that part which is surrounded by the erectile tissue of the corpus spongiosum. Its length is about six inches. The part contained within the bulb, sometimes distinguished as the *bulbous portion*, or sinus, is somewhat dilated. The succeeding portion, as far as the glans, is of uniform diameter, being intermediate in this respect between the bulbous and membranous portions. The cross section of its canal appears like a transverse slit. The canal of the urethra in the glans has, on the contrary, when seen in a cross section, the form of a vertical slit: in this part, which is from one-third to half an inch in length, the canal is again considerably dilated, forming what is named the *fossa navicularis*.

Lastly, at its orifice, which is a vertical fissure from $\frac{1}{5}$th to $\frac{1}{4}$th of an inch in extent, and bounded by two small lips, the urethra is again contracted and reaches its narrowest dimensions. From the resistant nature of the tissues at its margin, this opening does not admit so large a sound or catheter as even the membranous portion of the canal.

The **mucous membrane** of the urethra possesses a lining of epithelium, of which the superficial cells are long and columnar, except for a short distance (5 to 8 mm.) from the orifice, where they are squamous, and where the subjacent membrane is beset with papillæ. The epithelium rests on a basement membrane. Outside the mucous membrane there is a layer of convoluted vascular structure, and external to that a layer of circular plain muscular fibres separating it from the proper substance of the spongy body.

The whole lining membrane of the urethra, except near the orifice, is beset with small racemose mucous glands and follicles, commonly named the *glands of Littré*, the ducts of which pass obliquely forwards through the membrane. They vary much in size and in the extent to which their cavities are ramified and sacculated, some being quite simple. Besides these there are larger recesses or *lacunæ*, opening by oblique orifices turned forwards, or down the canal. These are most abundant along the floor of the urethra, especially in its bulbous part. One large and conspicuous recess, situated on the upper surface of the fossa navicularis, is named the *lacuna magna*. A median fold of the membrane rising from the inferior surface of this part of the urethra has been named the valve of the fossa navicularis.

Stratified concrements like those met with in the prostate are also found in old subjects in the glandular recesses of the urethra (Robin and Cadiat).

Cowper's glands.—In the bulbous portion of the urethra, near its anterior end, are the two openings of the ducts of *Cowper's glands*. These small glandular bodies (fig. 589, *c*) are seated above the bulb, behind the membranous portion of the urethra, between the two layers of the subpubic fascia, the anterior layer supporting them against the urethra. The arteries of the bulb pass above, and the transverse fibres of the compressor urethræ beneath these glands. They are two small firm rounded masses, about the size of peas, and of a deep yellow colour. They are compound racemose glands, composed of several

small lobules held together by a firm investment. This latter, as well as the walls of the ducts, contains muscular tissue. The epithelium of the acini consists of clear columnar cells, with a reticular protoplasm, staining like the cells of mucous glands. The ducts are lined with cubical epithelium. The ducts unite outside each gland to form a single excretory duct (fig. 589, *c d*). These ducts run forward near each other for about an inch or an inch and a half, first in the spongy substance and then beneath the mucous membrane, and terminate in the floor of the bulbous part of the urethra by two minute orifices opening obliquely. These glands secrete a viscid fluid, the use of which is not known; they appear to diminish in old age; sometimes there is only one present, and it is said both may be absent.

Occasionally there is a third glandular body in front of and between Cowper's glands; this has been named the *anterior prostate* or *ante-prostatic gland*.

The muscles in connection with the urethra and penis have been already described with the muscles of the perinæum in the first volume.

Recent Literature of the urethra and penis.—*Klein*, in Stricker's Handbook, 1871; *C. Langer*, in Wiener Sitzungsb., XLVI.; *Robin et Cadiat*, in Journ. de l'anat., 1875 (muqueuse urethrale); *Langerhans*, in Virch. Arch., LXI. (accessory genital glands); *Iversen*, in Nord. med. ark. XI. (prostate); *M. v. Frey*, in Arch. f. Anat., 1880 (corpora cavernosa); *Sehneidemühl*, in Zeitschr. f. Thiermed., VI., 1880 (Cowper's glands).

THE TESTES AND THEIR ACCESSORY STRUCTURES.

The *testes* or *testicles*, the two glandular organs which produce the spermatozoa, are situated in the pouch of integument termed the *scrotum*, each being suspended by the *spermatic cord*.

The **spermatic cord**.—The parts which form this cord are the excretory duct of the testes, named the vas deferens, the spermatic artery and veins, lymphatics, nerves, and connecting areolar tissue. Besides this last the cord has several coverings in common with the testis. The structures mentioned come together to form the cord at the internal or deep abdominal ring, and, extending through the abdominal wall obliquely downwards and towards the middle line, escape at the superficial or external abdominal ring, whence the cord descends over the front of the pubes into the scrotum.

The inguinal canal.—By the term inguinal canal is understood the space occupied by the spermatic cord as it passes through the abdominal wall. It extends from the deep to the superficial abdominal ring, and is about an inch and a half in length. In the upper part of this course the cord has the fascia transversalis behind it, and is covered in front by the lower fibres of the internal oblique and transversalis muscles; lower down it lies in front of the conjoined tendon of these muscles, the fibres of which have arched inwards over it, and its cremasteric covering is in contact anteriorly with the aponeurosis of the external oblique muscle. The inguinal canal is therefore said to be bounded posteriorly by the fascia transversalis above and the conjoined tendon below, and anteriorly by fibres of the transversalis and internal oblique muscles above, and the aponeurosis of the external oblique muscle below; while its floor is formed by the curving backwards of Poupart's ligament, and its roof by the apposition of the layers of the abdominal wall and the arched fibres of the internal oblique muscle.

As it enters the inguinal canal, the cord receives a covering from the

infundibuliform fascia, a thin layer continuous with the fascia transversalis, and prolonged down from the margin of the deep abdominal ring; within the canal it receives a covering from the cremaster muscle and its layer of fascia; and as it emerges from the canal there is added superficially to this, the intercolumnar fascia prolonged from the margin of the superficial abdominal ring.

The scrotum.—The *scrotum* forms a purse-like investment for the testes and part of the spermatic cords. Its condition is liable to some variations according to the state of the health and other circumstances: thus it is short and corrugated in robust persons and under the effects of cold, but becomes loose and pendulous in persons of weak constitution, and under the relaxing influence of heat. A superficial division into two lateral halves is marked by a slight median ridge, named the *raphe*, extending forwards to the under side of the penis, and backwards along the perinæum to the margin of the anus.

The coverings of the cord and testis in the scrotum may be enumerated from without inwards as follows, viz., the *skin*, *superficial fascia* and *dartos tissue*, the *intercolumnar fascia*, the *cremaster muscle* and *fascia*, and the *infundibuliform fascia*, which is united to the cord by a layer of loose areolar tissue; lastly, the special serous membrane of the testis named the *tunica vaginalis*, which forms a close sac, of which one part lines the scrotum and the other closely envelopes the testis.

1. The **skin** of the scrotum is very thin, and is of a darker colour than elsewhere; it is generally thrown into rugæ or folds, which are more or less distinct according to the circumstances already mentioned. It is furnished with sebaceous follicles, the secretion from which has a peculiar odour, and it is covered over with thinly scattered curled and flattened hairs, the bulbs of which may be seen or felt through the skin when the scrotum is stretched. The superficial blood-vessels are also readily distinguished through this thin integument.

2. Immediately beneath the skin of the scrotum there is found a thin layer of a peculiar loose reddish-brown tissue, endowed with contractility, and named the **dartos tunic.** This subcutaneous layer is continuous with the superficial fascia of the groin, perinæum, and inner side of the thighs, but assumes a different structure, and is entirely free from fat. The dartoid tissue, which is more abundant on the fore part of the scrotum than behind, forms two distinct sacs, for the corresponding testes, united together along the middle line so as to establish a median partition named the *septum scroti*, which is adherent below to the deep surface of the raphe, and reaches upwards to the root of the penis. The dartos is very vascular, and owes its contractile properties to the presence of a considerable amount of unstriped muscular tissue (Kölliker).

3. The **intercolumnar** or **spermatic fascia**, a very thin and transparent but relatively firm layer, derived from the tendon of the external oblique muscle of the abdomen, is attached above to the margins of the external ring, and is prolonged downwards upon the cord and testis. It lies at first beneath the superficial fascia, and lower down beneath the dartos, and it is intimately connected with the layer next mentioned.

4. The **cremasteric** layer is composed of scattered bundles of striped muscular fibres, connected together into a continuous covering by intermediate areolar membrane. The red muscular portion, which is continuous with the lower border of the internal oblique muscle of the abdomen, constitutes the *cremaster muscle*, and the entire covering is

named the *cremasteric fascia.* By the action of the cremaster the cord is shortened and the testicle is raised towards the body.

5. The **infundibuliform fascia**, continuous above with the *fascia transversalis* and the subperitoneal areolar membrane, and situated immediately beneath the cremasteric fascia, invests the cord completely, and is connected below with the posterior part of the testicle and the outer surface of its serous tunic. On forcing air beneath the infundibuliform fascia, a quantity of loose and delicate areolar tissue is seen to connect its deep surface with the vas deferens and spermatic blood-vessels, and to form lamellæ between them. This areolar tissue is continuous above with the subserous areolar tissue found beneath the peritoneum on the anterior wall of the abdomen ; below, it is lost upon the back of the testicle. Together with the infundibuliform fascia, it forms the *fascia propria* of Astley Cooper.

Lying amongst this loose areolar tissue, in front of the upper end of the cord, there is often seen a fibrous band, which is connected above with the pouch of peritoneum found opposite the upper end of the inguinal canal, and which passes downwards for a variable distance along the spermatic cord. Occasionally it may be followed as a fine cord, as far as the upper end of the tunica vaginalis ; sometimes no trace of it can be detected. It is the vestige of a tubular process of the peritoneum, which in the fœtus connects the tunica vaginalis with the

Fig. 591.

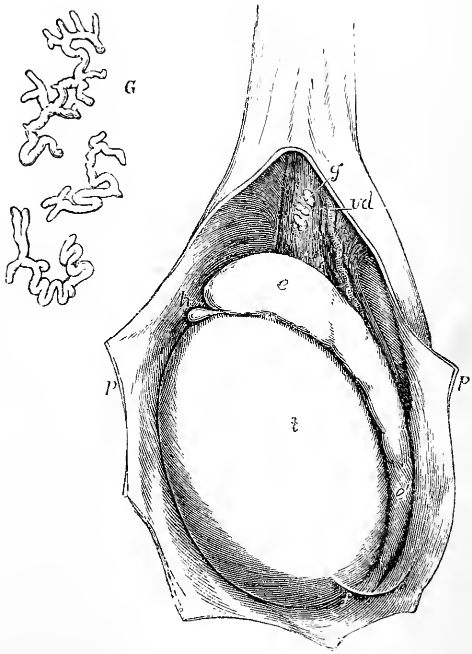


Fig. 591.—The left tunica vaginalis opened, showing the testis, epididymis, &c., from the outer side. (Allen Thomson.)

p, p, the cut edges of the parietal tunica vaginalis drawn aside ; *t,* the body of the testis ; *e, e',* the epididymis ; *f,* a fold of the tunica vaginalis passing from the body of the testis to the side. In the upper part of the figure the tunica vaginalis has been dissected off at the place of its reflection on the cord to show *v d,* the vas deferens, and *g,* the organ of Giradès ; G, the three small nodules of this organ enlarged about ten times, and showing the remains of tubular structure within them ; *h,* hydatid of Morgagni.

general peritoneal membrane. The testicle is placed within the abdomen during the greater part of fœtal life ; but at a period considerably prior to its escape from the abdominal cavity, a pouch of peritoneum already extends down into the scrotum. Into this pouch, or *processus vaginalis peritonæi,* the testicle projects from behind, supported by a duplicature of the serous membrane, named the *mesorchium.* Sooner or later after the gland has descended into the scrotum, the upper part or neck of this pouch becomes con-

tracted and finally obliterated, from the internal abdominal ring down nearly to the testicle, leaving no trace but the indistinct fibrous cord already described, while the lower part remains as a closed serous sac surrounding the testicle, and which is thence named the tunica vaginalis.

In the female fœtus an analogous pouch of peritoneum descends for a short distance along the round ligamemt of the uterus, and has received the appellation of the *canal of Nuck*. Of this traces may almost always be seen in the adult.

The neck of the processus vaginalis sometimes becomes closed at intervals only, leaving a series of sacculi along the front of the cord ; or a long pouch may continue open at the upper end, leading from the abdominal cavity into the inguinal canal. In other instances, the peritoneal process remains altogether pervious, and the cavity of the tunica vaginalis is thus made continuous with that of the peritoneum. In such a case of congenital defect, a portion of intestine or omentum may descend from the abdomen into the inguinal canal and scrotum, and constitute what is named a congenital hernia. Lastly, one or both testes may remain permanently within the abdomen, or their descent may be delayed till after puberty, when it may occasion serious disturbance. Retention of the testes in the abdomen (cryptorchismus) is, in many instances, the accompaniment of arrested development of the glandular structure ; it is, however, a peculiarity which may be present without impotence.

In a few mammals, as the elephant, the testes remain permanently within the abdomen ; in a much larger number, as the rodentia, they only descend at each period of rut. The complete closure of the tunica vaginalis is peculiar to man, and may be considered as connected with his adaptation to the erect posture.

6. The **tunica vaginalis.**—This tunic forms a shut sac, of which the opposite free surfaces are in contact with each other. Like the serous membranes in general, of which it presents one of the simplest forms, it may be described as consisting of a *visceral* and a *parietal* portion. The visceral portion, *tunica vaginalis testis,* closely invests the greater part of the body of the testis, as well as the epididymis, between which parts it is depressed in the form of a pouch (digital fossa), and lines their contiguous surfaces, and it adheres intimately to the proper fibrous tunic of the gland. Along the posterior border of the gland, where the vessels and ducts enter or pass out, the serous coat, having been reflected, is wanting. This portion of the serous covering frequently presents villous prolongations on the borders of the epididymis and upper end of the testis ; these processes, sometimes of considerable length, are covered in some places with cylindrical, in others with layers of flat epithelium.

The parietal or scrotal portion of the tunica vaginalis is more extensive than that which covers the body of the testis ; it reaches upwards, sometimes for a considerable distance, upon the spermatic cord, extending somewhat higher on the inner than on the outer side. It also reaches downwards below the testicle, which, therefore, appears to be suspended at the back of the serous sac, when this latter is distended with fluid ; a fold, or so-called ligament, being left projecting at the lower end of the epididymis (fig. 591, *f*).

Vessels and nerves of the scrotum and spermatic cord.—The arteries are derived from several sources. Thus, the two *external pudic* arteries, branches of the femoral, reach the front and sides of the scrotum, supplying the integument and dartos ; the *superficial perineal* branch of the internal pudic artery is distributed to the back part of the scrotum ; and, lastly, more deeply seated than either of these is a branch given from the epigastric artery, named *cremasteric*, which is chiefly distributed to the cremaster muscle, but also supplies small branches to the other coverings of the cord, and by its ultimate divisions anastomoses with the other vessels. The *artery of the vas deferens*, a long slender vessel derived from the superior vesical, accompanies the tube in its whole length. The **veins** accompany the arteries. The veins of the cord form the

spermatic or pampiniform plexus elsewhere described. The **lymphatics** pass into the inguinal lymphatic glands.

The **nerves** also proceed from various sources. Thus, the *ilio-inguinal*, a branch of the lumbar plexus issuing by the external abdominal ring, supplies the integuments of the scrotum; this nerve is joined also by a filament from the *ilio-hypogastric* branch of the same plexus: sometimes two separate cutaneous nerves come forward through the external ring. The two *superficial perineal* branches of the internal pudic nerve accompany the artery of the same name and supply the inferior and posterior parts of the scrotum. The *inferior pudendal*, a branch of the small sciatic nerve, joins with the perineal nerves, and with them is distributed to the sides and fore part of the scrotum. Lastly, the *spermatic branch of the genito-crural* nerve reaching the spermatic cord at the internal abdominal ring, passes with it through the inguinal canal, and supplies the fibres of the cremaster muscle, besides sending a few filaments to the other deep coverings of the cord and testicle.

THE TESTICLES.

The **testes**, or principal reproductive glands (διδυμος, ορχις), are suspended obliquely in the scrotum by means of the cord and membranes already described; they are usually placed at unequal heights, that of the left side being lower than the other. They are of an ovoid form, but are slightly compressed laterally, so that they have two somewhat flattened sides or faces, an upper and a lower end, an anterior and a posterior border. They are about an inch and a half long, an inch and a quarter wide from back to front, and nearly an inch thick from side to side. The weight of each varies from three-quarters of an ounce to an ounce, the left being often a little the larger of the two.

The front and sides of the testis, together with the upper and the lower ends, are free, smooth, and closely invested by the tunica vaginalis. The posterior border is attached to the spermatic cord, and it is here that the vessels and nerves enter or pass out. When the testis is suspended in its usual position, its upper end is directed obliquely forwards and outwards, as well as upwards, whilst the lower, which is rather smaller, has the opposite direction. It follows from this that the posterior or attached border is turned upwards and inwards, and the outer flattened face slightly backwards.

Fig. 592.

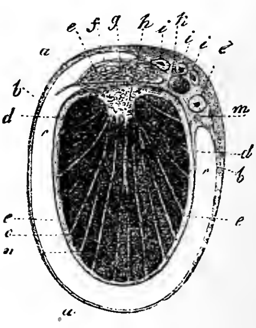


Fig. 592.—Transverse section through the right testicle and the tunica vaginalis (from Kölliker).

a, connective tissue enveloping the parietal layer of the tunica vaginalis; *b*, this layer itself; *c*, cavity of the tunica vaginalis; *d*, reflected or visceral layer adhering to *e*, the tunica albuginea; *f*, covering of epididymis (*g*) on the right or outer side; *h*, mediastinum testis; *i*, branches of the spermatic artery; *k*, spermatic vein; *l*, vas deferens; *m*, small artery of the vas deferens; *n*, *o*, septa or processes from the mediastinum to the surface.

Attached to the posterior border of the gland, and resting also on the neighbouring portion of its outer face, is a long narrow body, the *epididymis*, which forms part of the excretory apparatus of the testicle, and is principally composed of the convolutions of a long tortuous canal or

efferent duct, to be presently described. Its upper extremity, considerably larger than the lower, projects forwards on the upper end of the testis, and is named the *head* or *globus major* (fig. 591, *e*); the lower, which is more pointed, is termed the *tail* or *globus minor* (*e*′); whilst the intervening portion is named the *body*. The convex surface of the epididymis and the thin anterior border are free, and covered by the tunica vaginalis. The concave surface, or that directed towards the testis, except at the upper and lower ends, is also free, and invested by the same tunic, which here forms the digital pouch between the epididymis and the outer face of the testicle, and nearly surrounds the epididymis, except along its posterior border, which is united to the gland by a duplicature of the serous membrane, containing numerous blood-vessels. At its upper and lower extremity, the epididymis is attached to the testis by fibrous tissue and a reflection of the tunica vaginalis, the globus major also by the efferent ducts of the testis.

At the back of the testis and epididymis, beneath the fascia propria, opposite the lower two-thirds of the testis, is a considerable amount of unstriped muscular tissue, the *inner muscular tunic* of Kölliker.

On the front of the globus major, somewhat to the outer side, there are usually found one or more small pedunculated bodies covered by an extension of the tunica vaginalis and formed mainly by connective tissue and blood-vessels. These are the *hydatids of Morgagni.* They are commonly regarded as the remains of the fœtal structure termed Müller's duct. One of them of a more regularly pyriform shape, and more constant than the rest, lies closely between the head of the epididymis and the testis.

This has been thought, but as it would appear on insufficient evidence, to be the homologue of the ovary in the male sex (Fleischl, Krause). Its surface is ciliated, and a canal lined by ciliated epithelium and opening into the cavity of the tunica vaginalis is sometimes contained within it.

Structure of the Testis.—The testis is enclosed in a strong capsule, the **tunica albuginea.** This is a dense unyielding fibrous membrane, of a white colour, and of considerable thickness, which immediately invests the soft substance of the testis, and preserves the form of the gland. It

Fig. 593.

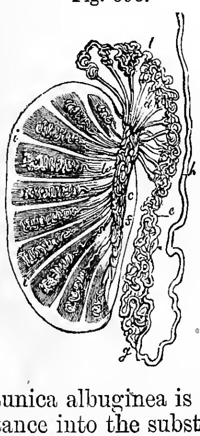


Fig. 593.—Plan of a vertical section of the testicle, showing the arrangement of the ducts.

The true length and diameter of the ducts have been disregarded. *a, a,* tubuli seminiferi coiled up in the separate lobes; *b,* vasa recta; *c,* rete vasculosum; *d,* vasa efferentia ending in the coni vasculosi; *l, e, g,* convoluted canal of the epididymis; *h,* vas deferens; *f,* section of the back part of the tunica albuginea; *i, i,* fibrous processes running between the lobes; *f* to *s,* mediastinum.

is composed of bundles of fibrous tissue, which interlace in every direction. The outer surface is covered by the tunica vaginalis, except along the posterior border of the testis, where the spermatic vessels pass through and the two extremities of the epididymis are attached.

In the interior, the fibrous tissue of the tunica albuginea is prolonged from the posterior border for a short distance into the substance of the gland, so as to form within it an incom-

plete vertical septum, known as the *corpus Highmori*, and named by Astley Cooper *mediastinum testis*. It extends from the upper nearly to the lower end of the gland, and it is wider above than below. The firm tissue of which it is composed is traversed by a network of seminal ducts, and by the larger blood-vessels of the gland, which are lodged in channels formed in the fibrous tissue.

From the front and sides of the corpus Highmori numerous slender fibrous cords and imperfect septa of connective tissue are given off in radiating directions, and are attached by their outer ends to the internal surface of the tunica albuginea at different points, thus incompletely dividing the glandular substance into lobules. According to Kölliker, plain muscular fibres are prolonged upon these septula. The whole internal surface of the tunica albuginea is covered by a multitude of fine blood-vessels, which are branches of the spermatic artery and veins, and are held together by a delicate areolar web. Similar delicate ramifications of vessels are seen on the various fibrous offsets of the mediastinum, upon which the blood-vessels are thus supported in the interior of the gland. This vascular network, together with its connecting areolar tissue, constitutes the *tunica vasculosa* of Astley Cooper.

The glandular substance of the testis which is included in the fibrous framework formed by the albuginea, the mediastinum and the trabeculæ is a mass of convoluted tubules known as the **tubuli seminiferi** which are somewhat loosely connected together by areolar tissue into the lobes or lobules above mentioned. Of these lobes there are some 300 or 400 (Krause); they are of unequal size, the middle ones being the larger; and are imperfectly separated from one another, the septa being incomplete. In each lobe are two, three or more seminiferous tubules closely convoluted, and here and there branched, especially at their anterior or distal extremity where, in a *cortical zone* near the albuginea, they frequently communicate laterally with one another. It is not difficult to unravel the tubules for some distance, for their walls are moderately strong, and their diameter ($\frac{1}{100}$th to $\frac{1}{150}$th of an inch) large compared with those of other tubular glands, such as the kidney. Their length is estimated to be on an average rather greater than two feet, and their number between 800 and 900 (Lauth). They have a smooth contour, but this is interrupted at intervals by small bulgings, which are more numerous near the commencement of a tubule than near its termination. The walls of the seminiferous tubules are composed of several layers of flattened cells. Of these only the innermost layer is complete, being formed of epithelioid cells closely united edge to edge into a basement membrane. This is strengthened by the other layers, which, however, exhibit intervals between the flattened cells which compose them, these intervals becoming very marked in the outermost layers. In consequence of their being thus formed of several layers, the walls of the tubules have a concentrically striated appearance in cross-section.

The tubules are occupied by an epithelium which consists of several irregular layers of cells, amongst which the seminal filaments or spermatozoa may be observed in different stages of development (fig. 594). In different tubules of the same testis and even in parts of the same tubule the condition of development of the spermatozoa may be very various, and the epithelium presents corresponding differences both in the number of its layers and the appearance of the cells.

In all cases, however, there is a complete or tolerably regular layer of cubical or somewhat flattened cells which immediately lines the basement membrane. A few of these *outer* or *lining cells* usually present indications of proliferation, the nucleus being in one of the phases characteristic of division, and here and there one of these cells may project between those of the next layer.

Within this stratum, in those parts where the formation of spermatozoa has progressed to its fullest extent (fig. 594, *c*), we come across an irregular layer of large clear rounded cells, many of which from the appearance of their nuclei are undergoing proliferation. They may be termed the *intermediate* or *proliferating cells*. They probably give origin to the cells of the third or *innermost* or *nutritive layer* which consists of a number of rows of granular ill-defined cells which appear blended with one another into an almost uniform mass. Their nuclei are small and faint, staining only slightly with logwood, and do not show evidence of undergoing proliferation; towards the lumen of the tubule they become very faintly outlined. Imbedded in the innermost part of this layer are the heads of the spermatozoa, whilst their tails project into and occupy the lumen of the tube, generally being bent down and extending for a short distance along its course.

Fig. 594.

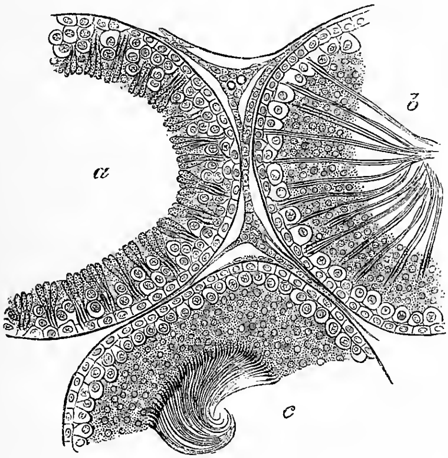


Fig. 594.—Section of parts of three seminiferous tubules of the rat (E.A.S., from a preparation by Mr. A. Frazer). Magnified.

a, with the spermatozoa least advanced in development; *b*, more advanced; *c*, containing fully developed spermatozoa. Between the tubules are seen strands of interstitial cells with blood-vessels and lymph-spaces.

It appears probable that the spermatozoa are set free by the breaking down into an albuminous fluid of the protoplasmic layer in which their heads are imbedded. In those parts of the seminiferous tubules and ducts where spermatozoa are free they are accompanied by nuclei and portions of nuclear substance, derived in all probability from the cells of this layer, the liquified protoplasm of which may be supposed to serve for the nutrition of the spermatozoa.

In other tubules, from which the spermatozoa have recently been discharged, the innermost layer is almost or entirely absent but the proliferating cells are two, three, or more rows deep. The formation of fresh spermatozoa appears to take place from some of these cells, groups of daughter-cells being formed by their proliferation, and each daughter-cell giving rise to a spermatozoon (fig. 594, *a*).

It is uncertain whether the lining-cells may not also produce spermatozoa; indeed, according to some authorities, they alone are concerned in the process (see below). Since, however, in any case the lining cells by their proliferation have originally given rise to the cells of the next layer, and probably continue to do so during life, the difference of opinion is not of so great importance as it at first sight may seem.

The nuclei of the cells which are concerned in the production of the spermatozoa (spermatoblasts) undergo division by the ordinary process of karyokinesis (see pp. 11 to 16) into two, four, or even more daughter-nuclei, which either separate from one another at once, each with a proportionate amount of the protoplasm of the mother-cell, or remain for a time enclosed within the mother-cell. From the daughter-nuclei the heads of the spermatozoa are developed, while the tails are formed from the enclosing protoplasm, but the exact mode of formation will be described after their structure has been treated of. It is in consequence of their development from a number of daughter-cells resulting from the proliferation of a mother-cell that the arrangement into groups is determined.

In the meantime the groups become more separated from one another by the accumulation between them of cells of the third or nutritive layer, which appear also to be produced by the proliferation of some of the intermediate cells. This is accompanied by a gradual shifting of the groups of spermatozoa towards the lumen, but for some time many of them remain with the heads buried in the outermost part of the nutritive layer and even between the cells of the intermediate layer (fig. 594, *b*). Eventually, however, they become entirely accumulated next the lumen, where they are more closely packed and the arrangement into groups becomes in a large measure obscured (fig. 594, *c*). These different conditions of the epithelium of the tubules can often be all observed in sections of adjacent tubules.

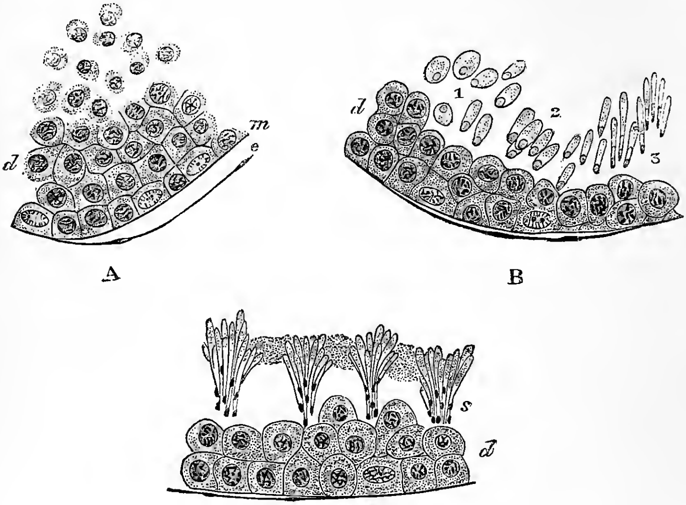
The above account of the appearances presented by the contents of the seminiferous tubules, which is the result of a renewed investigation of the subject,* differs in some respects from that of preceding writers. According to some authors, all the cells within the lining layer are spermatoblasts, the distinction between these and cells which simply serve for their support and nutrition not being recognized. According to most other authors, it is only the cells of the lining layer which give rise to spermatozoa; some of these cells (spermatoblasts of Ebner) growing towards the lumen between the cells of the inner layers as elongated columns terminating in enlarged extremities. Within the latter the nuclei multiply, and form daughter-nuclei, and from these and the protoplasm surrounding them the spermatozoa are developed, and are thus at first grouped together at the extremity of the elongated columns. The cells between serve simply for support and nutrition. As has already been stated, this view is not essentially different from the one adopted in the text; differing chiefly from that in insisting upon the permanent connection of the spermatoblasts with the lining epithelium.

Klein differs from most authors in describing the spermatozoa as becoming developed from completely separated daughter-cells (fig. 595, A, B), and as possessing at first no grouped arrangement, this being subsequently acquired (fig. 595, C), but in what manner is not explained. As to this view it may be remarked that there is no doubt the grouping appears more distinct in intermediate stages of development (as in fig. 594, *b*) than in the earliest stages; but that this seems to be owing to the accumulation of nutritive cells between groups of daughter cells, which are already existent, but which are at first so nearly in apposition that the eye fails to distinguish clearly the intervals between the groups.

* I have been much assisted in coming to a conclusion upon this question by the examination of specimens which were placed at my disposal by Mr. A. Frazer, M. B., Demonstrator of Anatomy in Owens College. (E.A.S.)

Lastly according to Sertoli and Merkel the columnar cells of v. Ebner and Neumann are not spermatoblasts but form part of a sustentacular cell-network which serves to support the rounded cells occupying the rest of the tubule, these latter being those which are actually concerned in the formation of the spermatozoa. Other observers, whilst admitting the existence of such a network, deny its continuity with the columnar cells.

Fig. 595.



C

Fig. 595.—Stages in the development of the spermatozoa of the dog (Klein).

m, membrana propria; *d*, epithelium; *e*, lamina of connective tissue; 1, 2, 3, daughter cells in different stages of development into spermatozoa; *s*, developing spermatozoa in groups.

Interstitial tissue, lymphatics, and blood-vessels.—The tissue which connects the seminiferous tubules is in some respects peculiar. It consists of fine fasciculi and laminæ of areolar tissue, these being covered by and partly composed of flattened epithelioid cells. Between the laminæ and fasciculi are large cleft-like spaces, containing lymph, and almost everywhere enclosing the basement membrane of the tubules. If these spaces are injected by the puncture-method, the injecting fluid flows away by the lymphatics of the spermatic cord. It is found to penetrate between the incomplete outer layers of the basement membrane, but is arrested by the innermost layer.

The blood-vessels are conducted at first along the trabeculæ, and from these they pass into the angular interstices between the tubules. Here they are supported by the areolar tissue and accompanied and often completely surrounded by tracts of peculiar epithelium-like polyhedral cells somewhat like the cortical cells of the suprarenal capsules, and like these often containing yellowish granules. They are known as the *interstitial cells* of the testis, and have been regarded as specially modified connective tissue (plasma-) cells (Waldeyer), or as epithelial cells derived from the Wolffian body (Klein), but until their development has been traced, nothing certain with regard to their nature can be stated. It may be remarked, however, that in sections of the fœtal testis, the

cells in question cannot be distinguished from the other cells of the developing intertubular connective tissue. Similar cells are met with in the stroma of the ovary.

The capillaries form a close network over the walls of the seminiferous tubules.

Ducts of the testis.—As the convoluted tubuli seminiferi approach the mediastinum testis they unite, as before said, with one another at acute angles into a smaller number of tubes which have a less flexuous course, and at length become nearly straight. Close to the mediastinum they taper into short, straight tubes (**tubuli recti**), of smaller diameter than the seminiferous tubes, and differing from them in the character of their epithelium (fig. 596). This, in the straight tubules, is a single layer of flattened or cubical cells continuous with the outer or lining cells of the seminiferous tubes. The basement membrane is also continued on to the straight tubules.

Fig. 596.

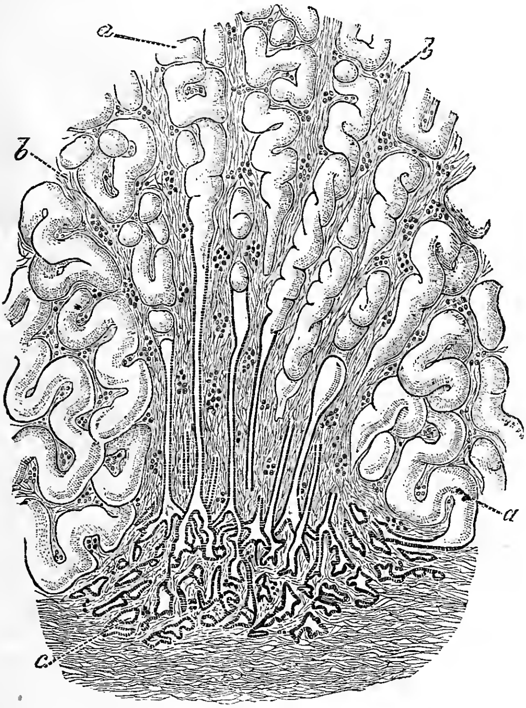


Fig. 597.

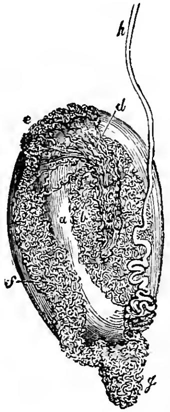


Fig. 596.—Passage of convoluted seminiferous tubules into straight tubules and of these into the rete testis (Mihalkovics).

a, seminiferous tubules; *b*, fibrous stroma continued from the mediastinum testis; *c*, rete testis.

Fig. 597.—Ducts of the testicle injected with mercury (from Haller).

a, body of the testicle; *b*, tubuli in the interior of the gland; *c*, rete vasculosum; *d*, vasa efferentia terminating in the coni vasculosi; *e*, *f*, *g*, convoluted canal of the epididymis; *h*, vas deferens ascending from the globus minor of the epididymis.

The straight tubules open into a network of vessels which lies in the substance of the mediastinum, and was named by Haller, **rete vasculosum testis** (fig. 596, *c*). The tubes composing the rete have no proper walls, but are merely channels in the fibrous stroma, lined by

flattened epithelium. Their diameter is greater than that of the tubuli recti. The secretion from the testis is accumulated in the rete, and is conducted to the upper and back part of the testis, whence it is conveyed away by the **efferent tubules**, or **vasa efferentia**. These are from twelve to fifteen, or sometimes twenty in number ; they perforate the tunica albuginea beneath the globus major of the epididymis, of which they may be said to form a part, and in the convoluted canal of which they ultimately terminate. On emerging from the testis, these vasa efferentia are straight, but, becoming more and more convoluted as they proceed towards the epididymis, they form a series of small conical masses, the bases of which are turned in the same direction, and which are named *coni vasculosi* (fig. 598, *f*). They are about $\frac{1}{50}$th of an inch in diameter. The largest of the cones is about two-thirds of an inch long, and when unrolled, each is found to consist of a single coiled duct, varying from six to eight inches in length, and the diameter of which gradually decreases from the testis to the epididymis (Huschke). Opposite the globus major these separate efferent vessels open, at intervals which, in the unravelled tube, are found to be about three inches in length, into a single canal or duct, the intervening and subsequent convolutions of which constitute the epididymis itself.

The **canal of the epididymis** (fig. 598, *g*) is disposed in very numerous coils, and extends from the globus major downwards to the globus minor or tail, where, turning upwards, it is continued on as the *vas deferens*. When its complicated flexuosities are unrolled, it is found to be twenty feet and upwards in length. The smallest windings are supported and held together by fine areolar tissue; but, besides this, numerous incomplete, transverse, fibrous partitions are interposed between larger masses of the coils, which have been named the *lobes* of the epididymis. The canal of the epididymis is, at its commencement, about $\frac{1}{70}$th of an inch in diameter, but diminishing as it proceeds towards the globus minor, it is about $\frac{1}{90}$th of an inch, after which it again

Fig. 598.

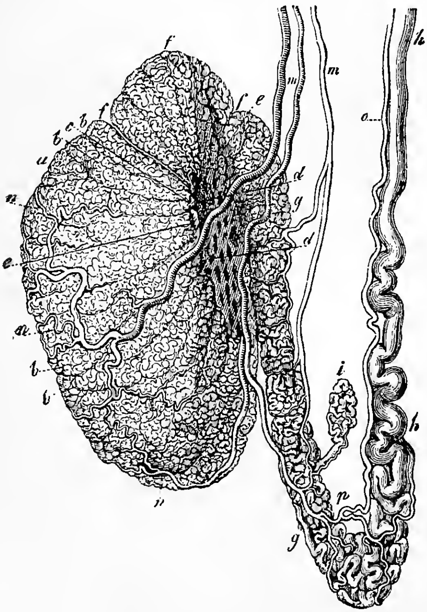


Fig. 598.—Injected testis epididymis, and vas deferens (from Kölliker after Arnold). $\frac{2}{1}$

a, body of the testicle ; *b*, lobules ; *c*, vasa recta ; *d*, rete vasculosum ; *e*, vasa efferentia ; *f*, coni vasculosi ; *g*, epididymis ; *h*, vas deferens ; *i*, vas aberrans ; *m*, branches of the spermatic artery passing to the testicle and epididymis ; *n*, ramification in the testis ; *o*, artery of the vas deferens ; *p*, its union with a twig of the spermatic artery.

increases in size, and becomes less deeply convoluted as it approaches the vas deferens. Its coats, which are at first thin, become thicker in its progress.

The vasa efferentia and the tube of the epididymis are provided with a considerable amount of plain muscular fibres in their wall. The epithelial lining cells are columnar or prismatic in form and are ciliated, the cilia being long, and causing by their movement a current in the outward direction. In the epididymis the cells are greatly elongated, in the vasa efferentia they are shorter ; in the lower part of the epididymis the cilia disappear. Between the fixed ends of the columnar cells other smaller cells are met with.

The **vas deferens** (fig. 598, *h*), or excretory duct of the testis, forms the continuation upwards of the convoluted canal of the epididymis. It commences at the lower end of the epididymis, and, at first rather tortuous but afterwards becoming straight, it ascends upon the inner side of the epididymis, and along the back of the testicle, separated from both, however, by the blood-vessels passing to and from the gland. Continuing then to ascend in the spermatic cord, the vas deferens accompanies the spermatic artery, veins and nerves, as far as the internal abdominal ring. Between the testicle and the external ring its course is nearly vertical : it lies behind the spermatic vessels, and is readily distinguished by its hard cord-like feel. It then passes obliquely upwards and outwards along the inguinal canal, and reaching the inner border of the internal abdominal ring, it leaves the spermatic vessels (which extend to the lumbar region), and turns suddenly downwards and inwards into the pelvis, crossing over the external iliac vessels, and turning round the outer or iliac side of the epigastric artery. Running beneath the peritoneum, it reaches the side of the bladder (fig. 577, *i*), upon which it descends, curving backwards and downwards to the hinder surface of that viscus, and finally passes forwards to the base of the prostate gland. In its course within the pelvis, it crosses over the cord of the obliterated hypogastric artery, and lies to the inner side of the ureter. Beyond this point, where it ceases to be covered by the peritoneum, it is attached to the coats of the bladder, in contact with the rectum, and gradually approaching its fellow of the opposite side. Upon the base of the bladder, the vasa deferentia are situated between two elongated receptacles, named the seminal vesicles (fig. 600) ; and, close to the base of the prostate, each vas deferens ends by joining with the duct from the corresponding seminal vesicle on its outer side to form one of the common seminal or ejaculatory ducts (fig. 590, 14).

The vas deferens measures nearly two feet in length. In the greater part of its extent it is cylindrical or slightly compressed, and has an average diameter of about one-tenth of an inch ; but towards its termination, beneath the bladder, it becomes enlarged and sacculated, forming the *ampulla* of Henle, and resembling in shape and structure a part of the seminal vesicle. Previously to its junction with the duct of that vesicle, it again becomes narrowed into a smaller and straight cylindrical canal. The walls of the vas deferens are very dense and strong, and feel hard to the touch, owing to the large proportion their thickness bears to the inner cavity of the tube, which is scarcely more than one-sixth of the whole diameter. In the sacculated portion the passage is much wider, and the walls are thinner in proportion. Small simple and branched tubular glands, similar to those of the vesiculæ seminales, beset the mucous membrane of this portion of the duct (Henle).

Besides an external areolar investment, and an internal mucous membrane, the vas deferens is provided with an intermediate thick muscular tunic, of a deep yellowish colour. This coat consists of two layers of plain fibres, an outer of longitudinal and an inner of circular fibres (fig. 599, *d*, *e*). In addition, near the commencement of the tube is an internal longitudinal stratum, extremely thin, and constituting not more than $\frac{1}{5}$th of the muscular coat (fig. 599, *c*).

The lining membrane exhibits on its surface three or four longitudinal ridges, and, besides this, in the sacculated portion of the duct, is marked by numerous finer rugæ which enclose irregular polyhedral spaces, resembling in this alveolar character the lining membrane of the seminal vesicles. The epithelium is of the columnar kind, and not ciliated. As in the epididymis there is a deeper layer of small cells between the columnar cells.

Fig. 599.

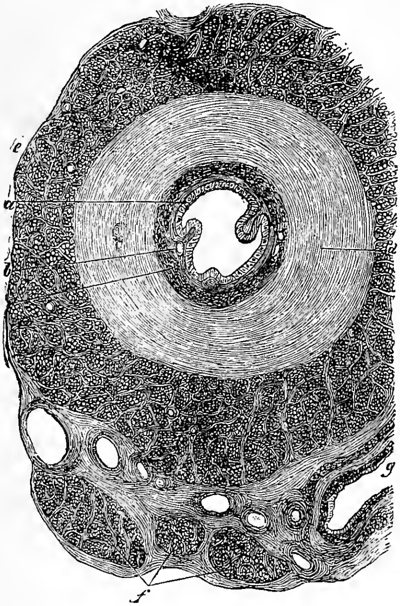


Fig. 599.—Section across the commencement of the vas deferens (Klein).

a, epithelium; *b*, mucous membrane; *c*, *d*, *e*, inner, middle and outer layers of the muscular coat; *f*, bundles of the internal cremaster muscles; *g*, section of a blood-vessel.

Vas aberrans.—This name was applied by Haller to a long narrow tube, or diverticulum (fig. 598, *i*), discovered by him, and almost invariably met with, which leads off from the lower part of the canal of the epididymis, or from the commencement of the vas deferens, and, becoming tortuous and convoluted, is rolled up into an elongated mass which extends upwards for an inch or more amongst the vessels of the spermatic cord, where the tube ends by a closed extremity. Its length, when it is unravelled, ranges from about two to twelve or fourteen inches; and its width increases towards its blind extremity. Sometimes this diverticulum is branched, and occasionally there are two or more such aberrant ducts. Its structure appears to be similar to that of the vas deferens. Its origin is probably connected with the Wolffian duct of the fœtus, but the exact mode of its formation and its office are unknown. Luschka states that occasionally it does not communicate with the canal of the epididymis, but appears to be a simple serous cyst.

Roth has described other small blind vasa aberrantia lying along the epididymis and connected with the rete testis.

Organ of Giraldès.—The small body thus named is situated in the front of the cord immediately above the caput epididymis (see fig. 591, *g*). It consists usually of several small irregular masses containing convoluted tubules lined with columnar ciliated epithelium, and is scarcely to be recognised until the surrounding connective tissue has been rendered transparent by re-agents. It has also received the name of *parepididymis*. Its tubules appear to be vestiges of part of the Wolffian body.

The **seminal vesicles** are two membranous receptacles, situated, one on each side, upon the base of the bladder, between it and the rectum. When distended, they form two long sacculated bodies, somewhat flattened on the side next the bladder, to which they are firmly attached, and convex on their inferior surface; they are widened behind and narrow in front (fig. 600, *s*). Their length is usually about two inches, and the greatest breadth about half an inch; but they vary both in size and shape in different individuals, and also on the two sides.

Their posterior obtuse extremities are separated widely from each

Fig. 600.

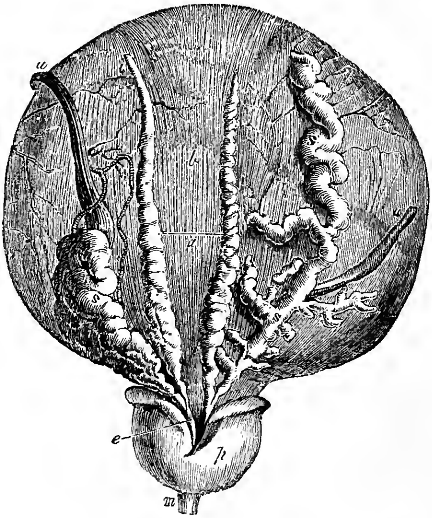


Fig. 600.—Base of the male bladder with the vesiculæ seminales, vasa deferentia, and prostate exposed (from Haller). $\frac{1}{2}$

a, line of reflexion of the peritoneum in the recto-vesical pouch; *b*, the part above this from which the peritoneum has been removed, exposing the longitudinal muscular fibres; *i*, left vas deferens ending in *e*, the left ejaculatory duct; *s*, left vesicula seminalis joining the same duct; the right vas deferens, and the right vesicula seminalis, marked *s*, *s*, and unravelled, are also shown; *p*, under side of the prostate gland, cut so as to exhibit the ejaculatory ducts; *m*, small part of the membranous portion of the urethra; *u*, *u*, the ureters, of which the right is turned to the side.

other, but anteriorly they converge so as to approach the two vasa deferentia, which run forwards to the prostate between them. With the vasa deferentia thus interposed, they occupy the two diverging sides of the triangular portion of the base of the bladder, which lies upon the rectum, and is bounded behind by the line of reflexion of the recto-vesical fold of the peritoneum. The seminal vesicles themselves also rest upon the rectum, but are separated from it by a layer of the recto-vesical fascia, which attaches them to the base of the bladder.

The sacculated appearance of the seminal vesicles is owing to their peculiar formation. Each consists of a tube somewhat coiled and repeatedly doubled on itself, and invested by dense fibrous tissue. When unrolled, this tube is found to be from four to six inches long, and about the width of a quill. Its posterior extremity is closed, so that it forms a long cul-de-sac; but there are generally, if not always, several longer or shorter branches or diverticula connected with it, which also end by closed extremities (fig. 600, *s*, *s*). Anteriorly the seminal vesicle becomes straight and narrowed, and ends opposite the base of the prostate by uniting on its inner side, at an acute angle, with the narrow termination of the corresponding vas deferens to form a single canal, which is the common seminal or ejaculatory duct.

In structure, the seminal vesicles resemble very closely the adjoining sacculated portions of the vasa deferentia. Besides an external investment, connected with the recto-vesical fascia, and containing vessels of considerable size, lymphatics, and gangliated nervous cords, they have a muscular coat and a mucous membrane. The muscular layers are thin compared with those of the vas deferens, and consist of three layers, an inner and outer longitudinal, and a middle layer of circular fibres. A considerable amount of plain muscular tissue is found covering the posterior surface and extending transversely between the two vesicles. There are also longitudinal fibres traceable over the vesicles from those of the bladder (Ellis, Henle). The mucous membrane is traversed by very many fine rugæ, which form an alveolar structure resembling that seen in the gall-bladder, but deeper and enclosing much finer meshes. The epithelium of the vesicles is columnar with a deep layer of small polyhedral cells.

The seminal vesicles serve as receptacles or reservoirs for the semen, as is proved by a microscopic examination of their contents; but, besides this, it is probable that they secrete a peculiar fluid which is incorporated with the semen.

The **common seminal** or **ejaculatory ducts**, two in number, are formed on each side by the junction of the narrowed extremities of the corresponding vas deferens and vesicula seminalis, close to the base of the prostate gland. From this point they run forwards and upwards, at the same time approaching each other, and then pass side by side through the prostate between its middle and two lateral lobes. After a course of nearly an inch, during which they become gradually narrower, they end in the floor of the prostatic portion of the urethra by two small slit-like orifices placed on the verumontanum, one on each prominent margin of the opening of the prostatic sinus (fig. 589, *d*). For a short distance the ejaculatory ducts run in the substance of the walls of the vesicle.

The coats of the common seminal duct, as compared with those of the vas deferens and vesicula, are very thin. The muscular coat consists of an outer thin circular and an inner longitudinal layer. The strong areolar tunic almost entirely disappears after the entrance of the ducts between the lobes of the prostate, but muscular fibres may be traced into the prostatic portion. The mucous membrane becomes gradually smoother as it passes into that of the urethra. Its epithelium is like that in the seminal vesicles and vas deferens. According to Henle, the muscular fibres of the duct are separated by blood-vessels as it passes through the prostate and form the trabeculæ of a layer of cavernous tissue.

These ejaculatory ducts convey the fluid contained in the seminal vesicles and vasa deferentia into the urethra. Their canal gradually narrows as they approach their termination, where its diameter is reduced to the $\frac{1}{50}$th of an inch.

Vessels and Nerves of the Testis.—The testicle and its excretory apparatus receive blood-vessels and nerves from sources which are different from those giving the vascular and nervous supply to the coverings of those parts.

The *spermatic artery*, or proper artery of the testicle, is a slender and remarkably long branch, which arises from the abdominal aorta, and passing down the posterior abdominal wall reaches the spermatic cord, and descends along it to the gland. In early fœtal life its course is much shorter, as the testis is then situated near the part of the aorta from which the artery arises. As the vessel

approaches the testicle, it gives off small branches to the epididymis, and then divides into others which perforate the tunica albuginea at the back of the gland, and pass through the corpus Highmori; some spread out on the internal surface of the tunica albuginea, whilst others run between the lobes of the testis, supported by the fibrous processes of the mediastinum. The smallest branches ramify on the delicate membranous septa between the lobes, before supplying the seminiferous tubes.

The vas deferens receives from one of the vesical arteries a long slender branch which accompanies the duct, and hence is named the *deferent artery*, or *artery of the vas deferens*. It ramifies on the coats of the duct, and reaches as far as the testis, where it anastomoses with the spermatic artery (fig. 598, *p*).

The *spermatic veins* commence in the testis and epididymis, pass out at their posterior border, and unite into larger vessels, which freely communicate with each other as they ascend along the cord, and form the *pampiniform plexus*. Ultimately two or three veins follow the course of the spermatic artery into the abdomen, where they unite into a single trunk, that of the right side opening into the vena cava, and that of the left into the left renal vein.

The *lymphatics* accompany the spermatic vessels and terminate in the lumbar lymphatic glands, which encircle the large blood-vessels in front of the vertebral column. As previously stated, they begin from intercommunicating lymph spaces which occupy the intervals between the tubuli seminiferi.

The *nerves* are derived from the sympathetic system. The *spermatic plexus* is a very delicate set of nervous filaments, which descend upon the spermatic artery from the aortic plexus. Some additional filaments, which are very minute, come from the hypogastric plexus, and accompany the artery of the vas deferens.

The vesiculæ seminales receive branches from the *inferior vesical* and *middle hæmorrhoidal arteries* and veins. The nerves belong to the sympathetic system, and come from the hypogastric plexus.

The semen.—The *semen* is a thick whitish fluid, the combined product of the testes and the accessory generative glands.

It contains floating in it, besides squamous and columnar epithelium-cells, a certain number of small highly refracting globules (*seminal granules*, Wagner), and the *spermatozoa* or spermatic filaments.

The *seminal granules* are colourless particles having an average diameter of about $\frac{1}{4000}$th of an inch. They stain deeply with most dyes, and are perhaps derived from the nuclei of the disentegrated nutritive cells of the seminiferous tubules.

Fig. 601.

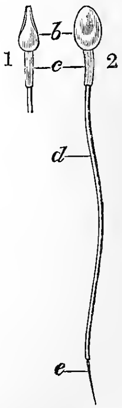


Fig. 601.—Human spermatozoa (Retzius).

1, in profile, the tail not represented; 2, viewed on the flat; *b*, head; *c*, middle-piece; *d*, tail; *e*, end-piece of the tail.

The **spermatozoa** are peculiar microscopic bodies which constitute the essential element for fecundation of the ovum. Each consists of a flattened oval part or so-called *head*, and a long slender filiform *tail* (fig. 601). At the junction of the head with the tail there may frequently be made out an intermediate portion, uniting the two. This is known as the *middle-piece* (Schweigger-Seidel). The head is about $\frac{1}{6000}$th of an inch long and $\frac{1}{10000}$th broad, and is thicker in its attached than in its free half, so that in profile it appears pointed (fig. 601, 1). There is a slight depression on each surface. The tail is from $\frac{1}{500}$th to $\frac{1}{400}$th of an inch in length.

It was long since shown by Leydig that in the spermatozoon of the salamander there occurs, attached to the tail, a delicate undulating membrane. A similar

membrane has been described by H. Gibbes in other vertebrates, including mammals, and he and Jensen also describe a long fine filament as bounding the membrane along its unattached border. This filament, which is attached to the head at one end, is considerably longer than the tail itself, so that it as well as the free edge of the membrane is thrown into undulating coils (see fig. 602). Retzius, who has still more recently investigated the subject, describes the tail as becoming abruptly narrowed near its extremity, which thus forms a distinct terminal portion (fig. 601, *c*); but he fails to detect the lateral membrane and filament in mammals.

Development of the spermatozoa.—The spermatozoa are developed within the seminiferous tubules from the daughter-cells of the spermatoblasts. The cell and its nucleus elongate and the latter passes towards the outer extremity, which becomes pointed. The protoplasm of the cell at first forms a clavate projection

Fig. 602.

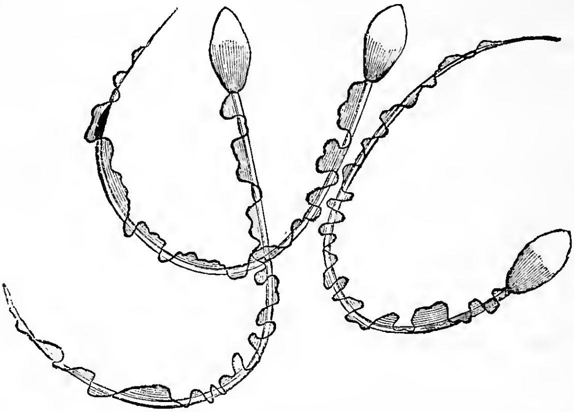


Fig. 602.—Human spermatozoa (H. Gibbes). Highly magnified. Somewhat diagrammatic.

towards the lumen (fig. 594, *a*). Between the nucleus and the more granular protoplasm is seen an intermediate portion of the cell composed of clear substance and partly embracing the pole of the nucleus (fig. 595, *b*). This appears to form eventually the middle piece of the spermatozoon whilst the nucleus of the cell (or at least the chromatic substance of the nucleus) becomes transformed into the head, and the granular clavate projection grows out into the tail. At early stages the head may appear covered by a transparent envelope, probably derived from the protoplasm of the cell (head-cap of Schweigger-Seidel). The development of the membrane and filament of Gibbes has not as yet been traced out, but fine filaments may often be seen coiled up within the daughter-cells which are undergoing transformation into spermatozoa, and it is not unlikely that these may be the filaments described by Gibbes, although they have usually been regarded as the developing tails of the spermatozoa (Kölliker). The membrane is probably a thinned out portion of the protoplasm of the cell.

Motion of the spermatozoa.—The spermatozoa, after their discharge or removal from the vas deferens or vesiculæ seminales, are found to exhibit active lashing movements of the tail with an undulating motion of the attached membrane and filament, lasting under favourable conditions for many hours. This action has the effect of causing them to progress in a somewhat spiral course through the fluid in which they float, and by it they are no doubt propelled upwards in the female generative passages and thus assisted to reach the ovum. The conditions under which the action of the spermatozoa is maintained and influenced are in almost all respects the same as those influencing the action of cilia (see pp. 51 to 54).

Recent Literature.—On the structure of the testis. *La V. St. George*, Article in Stricker's Handbook, 1871; *Hofmeister* in Wiener Sitzungsb. LXV., 1872; *Mihalkovics*, in Ludwig's Arbeiten, 1874; *Gerster* in Zeitschr. f. Anat. u. Entw. II. (lymphatics); *Stieda*, in Arch. f. mikr. Anat., XIV., 1877; *Messing*, Dissert., Dorpat, 1877. On the structure and development of the spermatozoa and on the epithelium of the seminiferous tubules especially. *Merkel* in Arch. f. Anat., 1871; and Med. Centralb., 1874; *v. Ebner*, in same journal, 1872; *Neumann* in Med. Centralbl., 1872, and in Arch. f. mikr. Anat., XI., 1875; *Blumberg*, Dissert., Wurzburg, 1873; *St. George*, various papers in Arch. f. mikr. Anat. X., XII., XV.; *Eimer* in Wurzb. Verhandl., 1874; *Miescher* in Basel Verhandl., 1874; *Bloch*, Dissert., Wurzburg, 1874; *Sertoli* in Gaz. med. lomb., 1875, and in Arch. p. l. sci. med. II., 1877: *v. Brunn* in Arch. f. mikr. Anat. XII., 1875; *Menzel* in Arch. f. klin. Chir. XXI., 1877; *Balbiani* in J. de micrographie, I. 1877; *Afanassiew* in Arch. f. mikr. Anat. XV., 1878 (stellate cells in epithelium); *Duval* in Gaz. méd., 1878; *H. Gibbes*, in Quart. journ. of micr. sci. 1879 and 1880; *Jensen* Die Structur des Samenfäden, Bergen, 1879; *Meyer*, in St. Petersb. Mem., 1879; *Helman*, Dissert., Dorpat, 1879; *Klein* in Med. Centralbl., 1880; *Brissaud* in Arch. de physiol., 1880; *Bloomfield* in Quart. journ. of micr. sci., 1880; *W. Krause* in Biol. Centralbl., 1881; *Retzius* in Biol. Untersuchungen, 1882.

On the ducts of the testes, and seminal vesicles. *Klein* in Stricker's Handbook, 1871; *Langerhans*, in Virch. Arch., LXI, 1874; *Robin et Cadiat*, in J. de l'anat., 1875; *Roth* in Zeitschr. f. Anat. u. Entw. II. 1876, and in Virch. Arch. LXXXI, 1880.

REPRODUCTIVE ORGANS IN THE FEMALE.

The reproductive organs in the female consist of the ovaries, uterus, and Fallopian tubes, which are named the *internal*, and the vagina, clitoris, nymphæ, labia, and other parts included in the vulva, named the *external* organs of generation.

THE VULVA,

The **vulva,** or **pudendum,** is a general term, which includes all the parts perceptible externally, viz., the mons Veneris, the labia, the hymen or carunculæ, the clitoris, and the nymphæ. The urethra also may be described in connection with these parts.

Integuments and Labia.—The integument on the fore part of the pubic symphysis, elevated by a quantity of areolar and adipose tissue, and covered with hair, is termed the *mons Veneris*. Two rounded folds of integument (*labia externa v. majora*, fig. 603, 20) extend downwards and backwards from below the mons, gradually becoming thinner; they leave an elliptic interval (*rima*) between them, the outer surface of each being continuous with the skin, and covered with scattered hairs, whilst the inner is lined by the commencement of the genito-urinary mucous membrane. Within the substance of the fold there is found, besides fat, vessels, nerves, and glands, a tissue resembling that of the dartos in the scrotum of the male, to which the labia in the main correspond. The labia majora unite beneath the mons and also in front of the perineum, the two points of union being called the anterior and posterior commissures. The posterior or inferior commissure is about an inch distant from the margin of the anus, this interval being the perineum of the female. Immediately within the posterior commissure, the labia are connected by a slight transverse fold (*frænulum pudendi*), which is frequently torn in the first parturition. The space between it and the commissure has been called *fossa navicularis*.

Clitoris.—Beneath the anterior commissure, and concealed between the labia, is the *clitoris* (fig. 603, 19), a small elongated body corresponding in conformation and structure to a diminutive penis, but differing in having no corpus spongiosum, nor urethra connected with it below.

It consists of two *corpora cavernosa*, which are attached by crura to the rami of the ischium and pubis, and are united together by their flattened inner surfaces so as to form an incomplete pectiniform septum. The body of the clitoris, which is about an inch and a half long, but is hidden beneath the mucous membrane, is surmounted by a small *glans*, consisting of spongy erectile tissue. The glans is imperforate, highly sensitive, and surrounded superiorly by a membranous fold, analogous

Fig. 603.

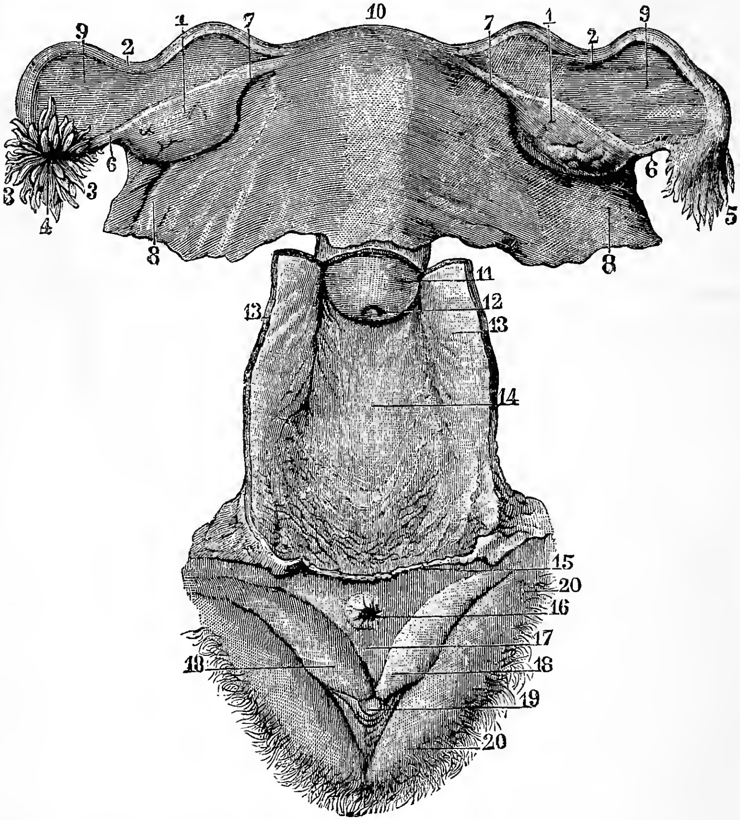


Fig. 603.—View of the female organs of generation from behind, the vagina being cut open and its walls turned aside (Sappey). $\frac{1}{2}$

1, Ovaries; 2, Fallopian tubes; 3, 4, 5, their fimbriated extremities (4 points to the ostium abdominale); 6, ovarian fimbria; 7, ligament of the ovary; 8, 9, broad ligaments; 10, uterus; 11, its vaginal portion; 12, os uteri; 13, lateral and posterior walls of vagina reflected; 14, its anterior wall; 15, edge of hymen; 16, orifice of urethra; 17, vestibule; 18, nymphæ; 19, clitoris; 20, labia majora.

to the prepuce. There is a small suspensory ligament attached to the upper border, like that of the penis, and in front of this the clitoris is dependent. The two ischio-cavernous muscles, named in the female *erectores clitoridis*, have the same connections as in the male, being inserted into the crura of the corpora cavernosa.

Nymphæ.—From the glans and preputial covering of the clitoris

two narrow pendulous folds of mucous membrane pass backwards for about an inch and a half, one on each side of the entrance to the vagina. These are the *nymphæ* (*labia interna v. minora*, fig. 603, 18). Their inner surface is continuous with that of the vagina; the external insensibly passes into the labia majora. They contain vessels between the laminæ of tegumentary membrane, but, according to Kobelt, no erectile plexus; for the erectile structure corresponding to the bulb and spongy body lies deeper, in two separate right and left halves, as will be presently explained.

Fig. 604.

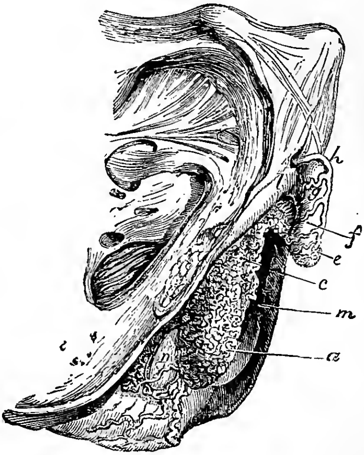


Fig. 604.—Lateral view of the erectile structures of the external organs in the female (from Kobelt). $\frac{2}{3}$

The blood-vessels have been injected, and the skin and mucous membrane have been removed; *a*, bulbus vestibuli; *c*, plexus of veins named pars intermedia; *e*, glans clitoridis; *f*, body of the clitoris; *h*, dorsal vein; *l*, right crus clitoridis; *m*, vestibule; *n*, right gland of Bartholin.

Vestibule.—Between the nymphæ is the angular interval called the *vestibule* (fig. 603, 17), in which is situated the circular orifice of the urethra, or *meatus urinarius* (16), about an inch below the clitoris and just above the entrance to the vagina. The membrane which surrounds this orifice is rather prominent in most instances so as readily to indicate its situation.

Immediately below the orifice of the urethra is the entrance to the vagina, which, in the virgin, is usually more or less narrowed by the *hymen* (15). This is a thin duplicature of the mucous membrane, placed at the entrance to the vagina; its form varies very considerably in different persons, but is most frequently semilunar, the concave margin being directed forwards towards the pubis. Sometimes it is circular, and is perforated only by a small round orifice, placed usually a little above the centre; occasionally it is cribriform, or pierced with several small apertures; and it may in rare instances completely close the vagina, constituting "imperforate hymen." On the other hand, it is often reduced to a mere fringe, or it may be entirely absent. After its rupture, some small rounded elevations remain, called *carunculæ myrtiformes*.

The **mucous membrane** may be traced inwards from the borders of the labia majora, where it is continuous with the skin: it forms a fold over the vascular tissue of the nymphæ, and is then prolonged into the urethra and vagina. It is smooth, reddish in colour, is covered by a scaly epithelium, and is provided with a considerable number of mucous crypts or follicles, and with glands which secrete an unctuous and odorous substance. The mucous crypts and follicles are especially distinct on the inner surface of the nymphæ, and near the orifice of the urethra. The sebaceous glands are found beneath the prepuce, and upon the labia majora and outer surface of the nymphæ.

The **glands of Bartholin** (or of Duverney) (fig. 604, *n*), correspond-

ing to Cowper's glands in the male, are two reddish yellow, round or oval bodies, measuring about half an inch in the longest diameter, lodged one on each side of the commencement of the vagina, between it and the erectores clitoridis muscles, beneath the superficial perineal fascia, and in front of the transverse muscles. Their ducts, which are long and single, run forward and open on the inner aspect of the nymphæ, outside the hymen or carunculæ myrtiformes.

Erectile tissue.—All the parts of the vulva are supplied abundantly with blood-vessels, and in certain situations there are masses composed of venous plexuses, or erectile tissue, corresponding to those found in the male. Besides the corpora cavernosa and glans clitoridis, already referred to, there are two large leech-shaped masses, the *bulbi vestibuli* (fig. 605, *a*), about an inch long, consisting of a network of veins, enclosed in a fibrous membrane, and lying one on each side of the vestibule, a

Fig. 605.

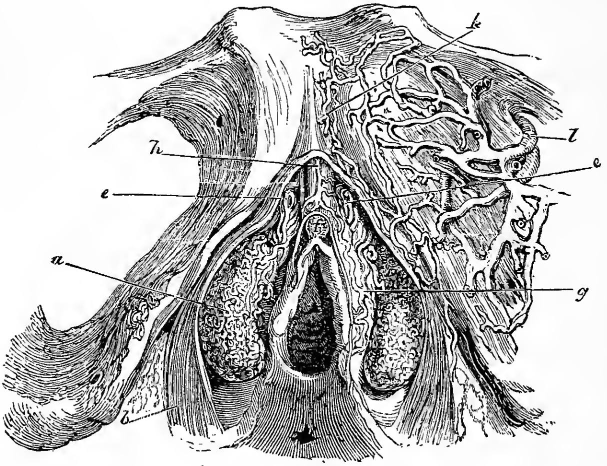


Fig. 605.—Front view of the erectile structures of the external organs in the female (from Kobelt). $\frac{2}{3}$

a, bulbus vestibuli; *b*, sphincter vaginæ muscle; *e*, *e*, venous plexus or pars intermedia; *f*, glans clitoridis; *g*, connecting veins; *h*, dorsal vein of the clitoris; *k*, veins passing beneath the pubes; *l*, the obturator vein.

little behind the nymphæ. They are rather pointed at their upper extremities, and rounded below: they are suspended, as it were, to the crura of the clitoris and the rami of the pubes, covered internally by the mucous membrane, and embraced on the outer side by the fibres of the constrictor vaginæ muscle. They are together equivalent to the bulb of the urethra in the male, which, it will be remembered, presents traces of a median division. In front of the bipartite bulb of the vestibule is a smaller plexus on each side, the vessels of which are directly continuous with those of the bulbus vestibuli behind, and of the glans clitoridis in front. This is the *pars intermedia* of Kobelt, and is regarded by him as corresponding with the part of the male corpus spongiosum urethræ which is in front of the bulb: it receives large veins coming direct from the nymphæ.

Blood-vessels.—The outermost parts of the vulva are supplied by the *superficial pudic and perineal arteries;* the deeper parts and all the erectile tissues receive branches from the *internal pudic arteries* as in the male. The veins also in a great measure correspond; there is a dorsal vein of the clitoris receiving branches from the glans and other parts as in the male: the veins of the bulbus vestibuli pass backwards into the vaginal plexuses, and are connected also with the obturator veins: above they communicate with the veins of the pars intermedia, those of the corpora cavernosa and the glans of the clitoris, and also with the vena dorsalis. The lymphatics accompany the blood-vessels.

Nerves.—Besides *sympathetic branches*, which descend along the arteries, especially for the erectile tissues, there are other nerves proceeding from the lumbar and sacral plexuses; those from the former being branches of the *genito-crural*, and those from the latter of the *inferior pudendal* and *internal pudic nerves*, which last sends comparatively large branches to the clitoris. They terminate in the clitoris in peculiar tactile corpuscles (see p. 164).

THE FEMALE URETHRA.

The **female urethra** is short as compared with that of the male sex. It is about an inch and a half in length; its average diameter is about $\frac{1}{4}$ to $\frac{1}{3}$ of an inch, but it is capable of great distension. Its direction is mainly downwards with a slight curvature forwards. It lies embedded in the anterior wall of the vagina, from which it can only be separated by dissection.

The external orifice, or *meatus urinarius* (fig. 603, 16), opens in the vulva, nearly an inch below and behind the clitoris, between the nymphæ, and immediately above the entrance to the vagina. From its orifice, which is its narrowest part, the canal passes upwards and backwards between the crura of the clitoris and behind the pubis, gradually enlarging into a funnel-shaped opening as it approaches and joins the bladder. There is also a dilatation in the back of the canal, just within the meatus.

The mucous membrane is whitish, except near the orifice; it is raised into longitudinal folds, which are not entirely obliterated by distension, especially one which is particularly marked on the lower or posterior surface of the urethra. Near the bladder the membrane is soft and pulpy, with many tubular mucous glands. Lower down these increase in size and lie in groups between the longitudinal folds; and immediately within and around the orifice, the lips of which are elevated, are several larger and wider crypts.

The lining membrane is covered with a stratified scaly epithelium, but near the bladder it becomes transitional. The submucous areolar tissue contains numerous elastic fibres. Outside this there is a highly vascular structure, in which are many large veins. Between the anterior and posterior layers of the triangular ligament, the female urethra is embraced by the fibres of the compressor urethræ muscle.

The *vessels* and *nerves* of the female urethra are very numerous, and are derived from the same sources as those of the vagina.

THE VAGINA.

The **vagina** is a dilatable membranous passage, extending from the vulva to the uterus, the neck of which is embraced by it (fig. 603). It rests below and behind on the rectum, supports the bladder and urethra in front, and is enclosed between the levatores ani muscles at the sides. It is slightly curved and is directed upwards and backwards: its axis corresponding below with that of the outlet of the pelvis, and higher up with that of the pelvic cavity. Its length is greater along the posterior

than along the anterior wall by about an inch and a half. The ends of the vagina are somewhat narrower than the middle part: the lower end, which is continuous with the vulva, is the narrowest part, and is widest from before backwards; the middle part is widest from side to side, being flattened from before backwards, so that its anterior and posterior walls are ordinarily in contact with each other: at its upper end it is rounded, and expands to receive the vaginal portion of the neck of the uterus. The vagina reaches higher up on the cervix uteri behind than in front, so that the uterus appears to be inserted into its anterior wall.

On the *inner surface* of the vagina, anteriorly and posteriorly, a slightly elevated ridge extends from the lower end upwards in the middle line, forming the *columns* of the vagina, or *columnæ rugarum.* Numerous dentated transverse ridges, called *rugæ*, are also observed, particularly in persons who have not borne children, running at right angles from the columns. These columns and rugæ are most evident near the entrance of the vagina and on the anterior surface, and gradually become less marked, and disappear towards its upper end.

Fig. 606.

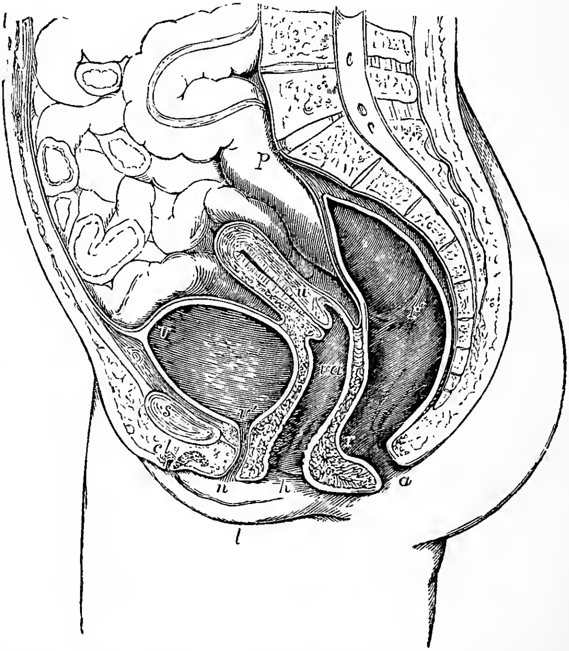


Fig. 606.—Sectional view of the viscera of the female pelvis (Allen Thomson, after Houston and from nature). $\frac{1}{4}$

The pelvic viscera having been distended and hardened with alcohol previously to making the section, are somewhat larger than natural and the vagina appears open, whereas its anterior and posterior walls should be in contact with one another. *p*, promontory of the sacrum; *s*, symphysis of the pubis; *v*, the upper part of the urinary bladder; *v'*, the neck; *v'*, *n*, the urethra; *u*, the uterus; *v a*, the vagina; *r*, third part of the rectum; *r'*, the fold between the middle and upper parts of the rectum; *a*, the anus; *l*, the right labium; *n*, the right nympha; *h*, the hymen; *cl*, the divided clitoris with the prepuce.

Structure and connections.—The walls of the vagina are thickest in front, in the vicinity of the urethra, which indeed may be said to be imbedded in the anterior wall of the vaginal passage; in other situations they are thinner. The vagina is firmly connected by areolar tissue to the neck of the bladder, and only loosely to the rectum and levatores ani muscles; at the upper end, for about a fourth part of its length, its posterior surface receives a covering from the peritoneum, which descends in the form of a cul-de-sac thus far between the vagina and the rectum.

Externally the vagina presents a coat of dense areolar tissue, and beneath this its walls are composed of unstriped muscle, which is not distinctly separable into strata, but is composed chiefly of fibres internally circular and externally longitudinal. Round the tube a layer of loose erectile tissue is found, which is most marked towards the vulva.

At its lower end, the vagina is embraced by striated muscular fibres, which constitute the *sphincter vaginæ*, already described.

The mucous membrane, besides the columns and rugæ, is provided with papillæ, and with numerous mucous glands, especially in its upper smoother portion and round the cervix uteri. It is lined with a stratified scaly epithelium.

Vessels and Nerves.—The vagina is largely supplied with vessels and nerves. The *arteries* are derived from branches of the internal iliac, viz., the *vaginal*, *internal pudic*, *vesical*, and *uterine*. The veins correspond; but they first surround the vagina with numerous branches, and form at each side a plexus named the *vaginal plexus*. The nerves are derived from the *hypogastric plexus* of the sympathetic, and from the *fourth sacral* and *pudic nerves* of the spinal system; the former are traceable to the erectile tissue.

THE UTERUS.

The **uterus** or **womb**, (*matrix*, ὑστερον,) is a hollow muscular organ, with very thick walls, situated in the pelvic cavity between the rectum and the urinary bladder. In the case of pregnancy the uterus receives the ovum, retains and supports it during the development of the fœtus, and expels it at the time of parturition. The Fallopian tubes, extending from each upper angle of the uterus to their ovarian opening, conduct the ovum from the ovary to the uterine cavity. During gestation, the uterus undergoes a great enlargement in size and capacity, as well as important structural changes.

In the fully developed virgin condition, which is that to which the following description mainly applies, it is a somewhat pear-shaped body, flattened from before backwards, free above, and connected below with the vagina, into which its lower extremity projects (fig. 603). It does not reach above the brim of the pelvis. Its upper end is directed upwards and forwards, the lower downwards and backwards; so that its axis corresponds with that of the inlet of the pelvis, and forms an angle or sudden curve with the axis of the vagina, which corresponds more nearly with that of the outlet of the cavity. The uterus projects upwards into a fold of the peritoneum, by which the body is covered both before and behind, and the neck also behind; but in front the peritoneum does not descend farther than the body. Its free portion is in contact with the other pelvic viscera, some convolutions of the small intestine usually lying upon its upper and posterior surface. Its lower and anterior surface is in contact with the bladder, with the intervention of the peri-

toneal pouch. From its two sides the peritoneum is reflected in the form of a duplicature, named the broad ligament.

The average dimensions of the uterus are about three inches in length, two in breadth at its upper and wider part, and nearly an inch in thickness: its weight is from seven to twelve drachms. It is usually described as possessing a fundus, body, and neck.

Fig. 607.

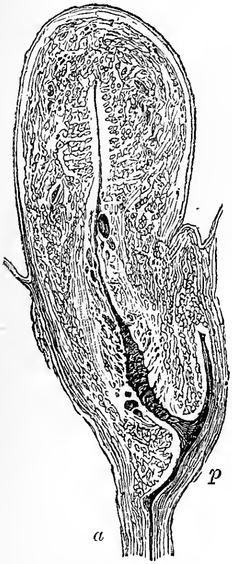


Fig. 607.—Sagittal section through the uterus and the upper end of the vagina (Henle).

a, anterior ; *p*, posterior wall of the vagina.

The *fundus* is the broad bulging upper end of the body, and projects upwards from between the points of attachment of the Fallopian tubes (fig. 603, 10). The *body* gradually narrows as it extends from the fundus to the neck; its sides are nearly straight; its anterior and posterior surfaces are both somewhat convex, but the latter more so than the former. At the points of union of the sides with the rounded superior border are two projecting angles, with which the Fallopian tubes are connected, the round ligaments being attached a little before, and the ovarian ligaments behind and beneath them; these three parts are all included within the peritoneal duplicature of the broad ligaments (fig. 603, 8). The body of the uterus is of a less rigid consistence than the neck and readily becomes bent somewhat upon it either forwards or backwards, following to a great extent the condition of distension of the bladder. When the latter is empty the body of the uterus may be nearly horizontal. The *neck*, or *cervix uteri*, narrower and more rounded than the rest of the organ, is nearly an inch in length; it is continuous above with the body, and, becoming somewhat smaller towards its lower extremity projects into the upper end of the tube of the vagina, which is united all round with the substance of the uterus, but extends upwards to a greater distance behind than in front. The projecting portion of the uterus is named the *vaginal part* (fig. 603, 11). The axis of the cervix uteri may be in the same direction with that of the vagina, in which case the amount of flexion between the body and neck is greater, or it may be directed forwards and form an angle with the direction of the vagina. The lower end of the uterus presents a transverse aperture, by which its cavity opens into the vagina (fig. 603, 12); this is named variously *os uteri, os uteri externum*, and (from a supposed likeness to the mouth of the tench fish) *os tincæ*. It is bounded by two thick lips, the posterior of which is the thinner and longer of the two, while the anterior, although projecting less from its vaginal attachment, is lower in position, and, when the tube is closed, comes into contact with the posterior wall of the vagina (fig. 607). These borders or lips are generally smooth, but, after parturition, they frequently become irregular, and are sometimes fissured or cleft.

Cavity of the uterus.—The walls of the uterus are of great thickness.

and the cavity is thus proportionately much reduced in size. The part within the body is triangular (fig. 608), and flattened from before backwards, so that its anterior and posterior walls touch each other (fig. 607). The base of the triangle is directed upwards, and is convex towards the interior of the uterus. The cavity, narrowing gradually, is prolonged into its two superior angles, at each of which it leads by a minute foramen into the narrow canal of the Fallopian tube. At the junction of the body with the neck, the cavity is slightly constricted,

Fig. 608.

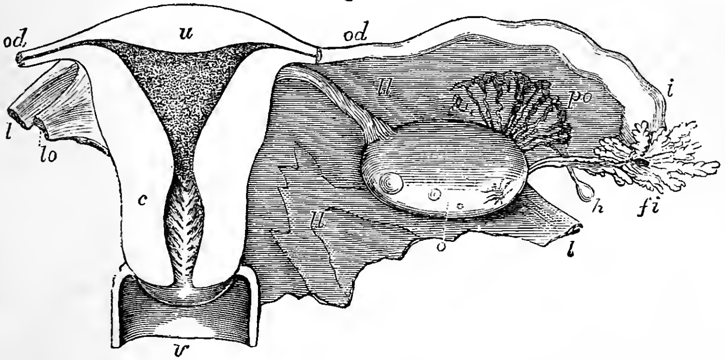


Fig. 608.—Diagrammatic view of the uterus and its appendages, as seen from behind. (A. T.) $\frac{2}{3}$

The uterus and upper part of the vagina have been laid open by removing the posterior wall; on the left side the Fallopian tube, round ligament, and ovarian ligament have been cut short, and the broad ligament removed; *u*, the fundus of the uterus; *c*, the cervix opposite the os internum; the triangular shape of the uterine cavity is shown, and the dilatation of the cervical cavity with the rugæ termed arbor vitæ; *v*, upper part of the vagina; *od*, Fallopian tube or oviduct; *l*, round ligament; *lo*, ligament of the ovary; *o*, ovary (here represented with its long axis horizontal although in the natural position within the body it is oblique or nearly vertical); *i*, wide outer part of the right Fallopian tube; *fi*, its fimbriated extremity; *po*, parovarium; *h*, one of the hydatids frequently found connected with the broad ligament.

and thus forms what is sometimes named the *internal orifice* (*os uteri internum, isthmus vel ostium uteri*); this opening is often smaller than the os externum, and is of a circular form. That portion of the cavity which is within the neck is tubular and slightly flattened before and behind; it is somewhat dilated in the middle, and opens inferiorly into the vagina by the os tincæ. Its inner surface is marked by two longitudinal ridges or columns, which run, one on the anterior, the other on the posterior wall, and from both of which rugæ are directed obliquely upwards on each side, so as to present an appearance which has been named *arbor vitæ uterinus*, or *palmæ plicatæ* (fig. 608): this structure is most strongly marked anteriorly.

Structure.—The walls of the uterus consist of an outer serous covering, an inner mucous membrane, and thick intermediate muscular substance. The serous covering or *peritoneal* layer has been already referred to.

The thick middle part of the wall of the uterus is of firm consistence: being mainly composed of plain muscular fibres of small size, $\frac{1}{110}$ inch in length, in the unimpregnated uterus, but greatly enlarged (to $\frac{1}{40}$th inch) in the gravid state. These fibres interlace closely with each other,

but are disposed in bundles and layers, and are intermixed with areolar tissue, a large number of blood-vessels and lymphatics, and some nerves. The areolar tissue is more abundant near the outer surface. The arrangement of the muscular fibres is best studied in the uterus at the full period of gestation, in which the bundles become augmented in size. They may be referred to three sets of which the two more external may be regarded as corresponding with the muscular coat of other hollow viscera, whereas the internal is an immensely hypertrophied *muscularis mucosæ*, and will accordingly be described with the mucous membrane.

Muscular coat.—The *external layer* of the muscular coat forms a thin superficial sheet immediately beneath the peritoneum, and incomplete strata situated more deeply. A large share of these fibres, beginning as longitudinal bands at the cervix, arch transversely and obliquely over the fundus and adjoining part of the body of the organ, and pass on each side into the broad ligament. Of these some converge at either side towards the commencement of the round ligaments, along which they are in part prolonged to the groin; others pass off to the Fallopian tubes, and strong transverse bands from the anterior and posterior surfaces are extended into the ovarian ligaments. Other fibres run back from the cervix uteri beneath the recto-uterine folds of the peritoneum. The *inner layer* of the muscular coat, which is also thin, is composed of fibres which are found chiefly on the back of the uterus, and stretch over the fundus and towards the sides, running somewhat irregularly between the ramifications of the blood-vessels. The muscular coat proper seldom exceeds $\frac{1}{4}$ inch in thickness altogether, but it is not easy to assign its limits exactly, for there is little or no submucous areolar tissue forming a distinct coat as in most of the hollow viscera. It is chiefly the place of ramification of the blood-vessels before they pass into the mucous membrane that determines the boundary between the muscular layer of the mucous membrane and the muscular coat proper (J. Williams).

Fig. 609.

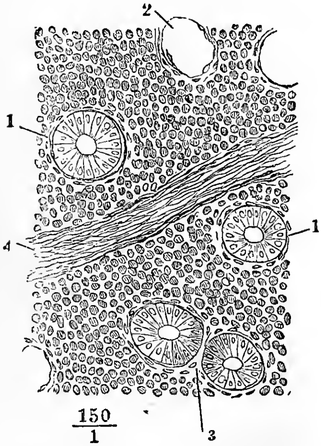


Fig. 609.—Section of the uterine mucous membrane parallel to the surface (Henle). $\frac{150}{1}$

1, 2, 3, glands (the epithelium has fallen out from 2); 4, a blood vessel.

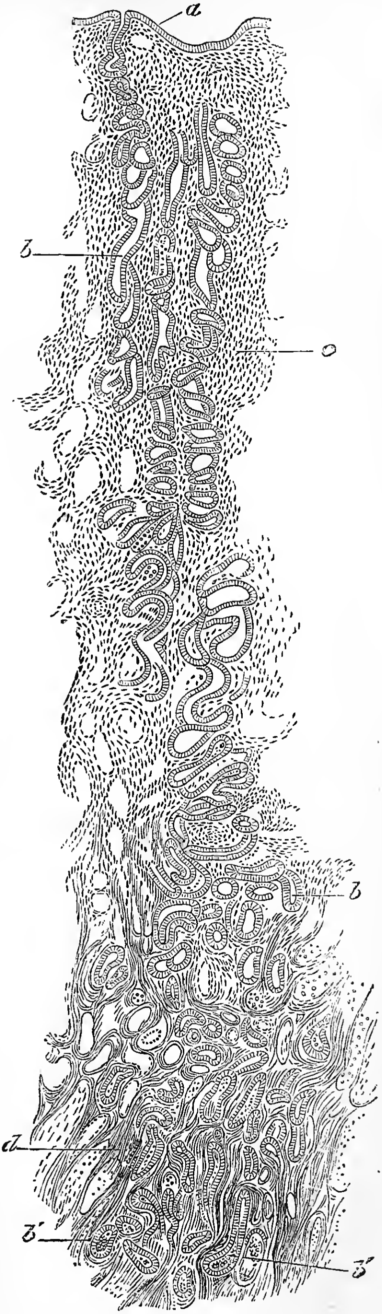
Mucous membrane.—The mucous membrane of the uterus is characterized by the enormous hypertrophy of the muscular layer proper to it—the muscularis mucosæ; indeed it is this which forms the greater part of the thickness of the uterine wall. The presence of this mass of plain muscular tissue in it confers a distinct character on the outer part of the membrane, so that in sections it is distinctly differentiated from the inner part or corium.

Muscularis mucosæ.—This consists of bands of fibres which are disposed with comparative regularity in its upper part, being arranged there in numerous concentric rings round the openings of the two Fallopian

Fig. 610.—Section of the mucous membrane of the uterus from near the fundus (adapted by J. C. Ewart from a figure by J. Williams).

a, epithelium of inner surface; *b*,*b*, uterine glands; *c*, interglandular connective tissue; *d*, part of the muscularis mucosæ with the ends of the glands, some of which, *b'*, are entirely filled by epithelium cells. This specimen was prepared from the uterus of a young woman who was accidentally killed three or four days before the expected appearance of the menstrual flow.

Fig. 610.



tubes, the widest circles of the two series meeting from opposite sides in the middle of the uterus. In the lower part of the body, and in the cervix the internal fibres run more transversely. They form the so-called sphincters of the os internum and os externum. At the neck, however, there are also longitudinal fibres within the transverse.

Corium.—As regards its inner part or corium the mucous membrane lining the cavity of the body differs greatly from that of the cervix, a distinct line of demarcation separating the two parts at the isthmus.

The *mucous membrane of the body* of the uterus is smooth, except during the menstrual period, and in the unimpregnated state is entirely devoid of ridges; it is of a peculiar soft spongy consistence, and of a dull, reddish colour.

Under the microscope it appears composed in great measure of small rounded, spindle-shaped, or irregular cells imbedded in a homogeneous ground-substance and with but few connective tissue fibres (figs. 609, 610). According to Leopold, however, there are numerous fibres, and they form a spongework with lymphatic spaces in the meshes. The inner surface is everywhere covered by columnar ciliated epithelium, and is beset, but somewhat sparingly, by the orifices of the uterine glands (fig. 610, *b*). These which were discovered by Sharpey,

are simple tubes bounded by a basement membrane and lined with ciliated columnar cells like those covering the inner surface. They pass usually obliquely and often with an irregular or convoluted course into the deeper part of the mucous membrane, and there terminate by blind, sometimes forked extremities, which are situated amongst the bundles of the muscularis mucosæ. Towards their extremities the uterine glands are entirely filled by cells (fig. 610, *b*), but in the greater part of their extent they present a distinct lumen.

The *membrane of the cervix* is much firmer and more fibrous than that of the body. Between the rugæ of the *arbor vitæ* there are numerous saccular and tubular glands. In the lower part of the cervix the mucous membrane is beset with vascular papillæ, and the epithelium is stratified, but in the upper half or more the epithelium is columnar and ciliated like that of the body. The glands, which are short, with a large lumen, are everywhere lined with columnar ciliated epithelium, even where the epithelium of the surface is stratified. Besides the follicular glands there are also the so-called *ovula Nobothi,* clear or yellowish vesicles of variable size, but visible to the naked eye, embedded in the membrane. These may arise from closed and distended follicles ; but their exact nature is still doubtful.

During pregnancy the mucous glands of the cervix secrete a considerable quantity of tenacious mucus, which effectually closes the passage downwards from the uterine cavity.

The surface of the os uteri is covered, like the vaginal portion, with stratified epithelium which conceals the vascular papillæ. It is destitute of glands.

LIGAMENTS OF THE UTERUS.—Where the peritoneum is reflected from the uterus to the bladder in front, and to the rectum behind, it forms, in each position, two semilunar folds, named respectively, the *vesico-uterine,* and the *recto-uterine folds*, or sometimes the *anterior* and the *posterior ligaments* of the uterus.

The *broad ligaments* (figs. 603, 608), are formed on each side by a fold or double layer of the peritoneum, which is directed laterally outwards from the anterior and posterior surfaces of the uterus, to be connected with the sides of the pelvic cavity. Between the two layers of the serous membrane are placed, firstly, the Fallopian tube, which runs along the upper margin of the broad ligament ; secondly, the round ligament, which is a little farther down and lies anteriorly ; thirdly, on the posterior surface, the ovary and its ligament, which lie in a special extension of the ligamentum latum ; and, lastly, throughout the greater part of the broad ligament, blood-vessels, lymphatics, and nerves, with fibres spreading from the superficial muscular layer of the uterus. The *ligament of the ovary* is merely a dense fibro-areolar cord, containing some uterine muscular fibres, and measuring about an inch and a half in length, which extends from the inner (or, in the natural position, lower) end of the ovary to the upper angle of the uterus, which it joins immediately behind and below the point of attachment of the Fallopian tube ; it causes an elevation of the posterior layer of the serous membrane, and, together with the ovary itself, forms the lower limit of a triangular portion of the broad ligament, which has been named the *ala vespertilionis* or bat's wing.

The *round ligaments* are two flat, cord-like bundles of fibres, about four or five inches in length, attached to the upper angles of the uterus, one on either side, immediately in front of the Fallopian tube. From

this point each ligament proceeds upwards, outwards, and forwards, to gain the internal inguinal ring, and after having passed, like the spermatic cord in the male, through the inguinal canal, reaches the fore part of the pubic symphisis, where its fibres expand and become united with the substance of the mons Veneris. Besides areolar tissue and vessels, the round ligaments contain, chiefly in their inner third, plain muscular fibres, which are prolonged into them from the outer muscular layer of the uterine wall. Each ligament also receives a covering from the peritoneum, which, in the young subject, projects under the form of a tubular process for some distance into the inguinal canal ; this, which resembles the processus vaginalis originally existing in the same situation in the male, is named the canal of Nuck ; it is generally obliterated in the adult, but is sometimes found even in advanced life.

Vessels.—The *arteries of the uterus* are four in number, viz., the right and left *ovarian* (which correspond to the spermatic of the male) and the *uterine.* Their origin, as well as the mode in which they reach the uterus and ovaries, has been described in the first volume. They are remarkable for their frequent anastomoses, and also for their singularly tortuous course. After passing a short distance into the thickness of the uterine wall they divide into branches, which penetrate the muscular tissue of the mucous membrane, supplying it with capillaries, and then pass towards the inner portion of the membrane and open into a network of large capillaries which pervades the tissue in that situation, and are especially developed near the surface and around the glands. In the cervix however, and especially in the vaginal portion, the arteries, which in this situation possess walls of considerable thickness, after entering the mucous membrane, divide into a number of small branches which pass directly towards the surface and open into the capillary network there present, from which loops pass into the papillæ. The *veins* correspond with the arteries ; they are very large, and form plexuses of sinus-like vessels, with thin walls in immediate contact with the uterine tissue. The *lymphatics* commence according to Leopold as cleft-like spaces in the mucous membrane, but there are also well-marked lymphatic vessels extending as a plexus through the whole thickness of the membrane (Hoggan). These open into plexuses of vessels in the muscularis mucosæ and muscular coat proper ; and these again are in communication with valved vessels beneath and in the serous covering.

Nerves.—The nerves are derived from the *inferior hypogastric plexuses*, the *spermatic plexuses*, and the *third* and *fourth sacral nerves.* They consist of both medullated and non-medullated fibres, and in animals small ganglia have been observed in the submucous tissue, connected with the non-medullated fibres.

Periodic structural changes in the Uterus.—The changes which accompany menstruation and gestation may be shortly indicated here.

At each successive recurrence of *menstruation* a complete removal of the superficial part of the mucous membrane takes place by a process of softening and molecular disintegration which commences, along with the menstrual discharge, close to the cervix, or at the os internum, and advances progressively towards the fundus during the remaining days of the flow of blood (J. Williams). Previous to this change, there is a greatly increased general vascularity of the parts, and the mucous membrane becomes very much thicker. The process of disintegration reaches as far as the inner fibres of the muscularis mucosæ ; and the hemorrhage is the direct result of the destruction and open condition of the small vessels.

The process of restoration of the uterine membrane, which begins even before the cessation of the menstrual flow, proceeds in the same order, from the lower end upwards to the fundus, and consists in a very rapid proliferation of the cells and nuclei which occupy the interstices of the inner muscular fibres, and among which are embedded the deepest parts of the utricular glands. The lining membrane of the cervix does not participate in the changes referred to.

In *gestation* more extensive alterations ensue. The weight of the organ increases from about one ounce to a pound and a half or even three pounds. Its colour becomes darker, its tissue less dense and its muscular bundles more evident. A very great increase takes place in the muscular tissue, this increase being mainly the result of the enlargement of the already existing elements, the cells becoming enlarged to the extent of from seven to eleven times in length, and from two to five times in breadth (Kölliker). A formation of new cells is also said to occur mainly in the innermost layers, and to continue until the sixth month of pregnancy, when it ceases. The round ligaments become enlarged, and their muscular structure more marked; the broad ligaments are encroached upon by the intrusion of the growing uterus between their layers. The mucous membrane and the glands of the body of the uterus undergo an enlargement very similar to that which precedes menstruation, and they subsequently become the

Fig. 611.

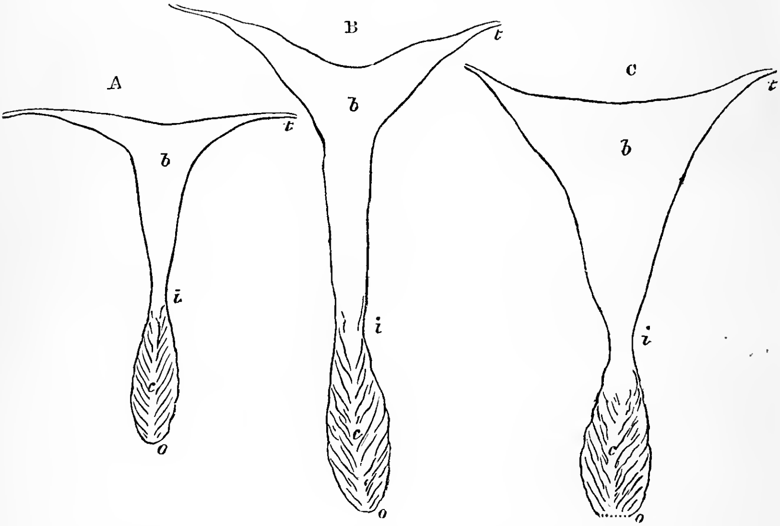


Fig. 611.—Outlines of moulds of the uterine cavity in different states (after F. Guyon). Natural size.

A, in a virgin of 17 years of age; B, in a woman of 42 years who had not borne children; C, in a woman of 35 years who had borne children; *b*, cavity of the body; *c*, that of the cervix; *i*, the isthmus or os internum; *o*, os externum; *t*, passage of the upper angle into the Fallopian tube.

seat of peculiar changes, to be more particularly stated under Development whilst the membrane of the cervix loses its columns and rugæ. The blood-vessels and lymphatics are greatly enlarged, and it is observed that the arteries become exceedingly tortuous as they ramify upon the organ. The nerves also undergo considerable increase in size.

After parturition, the uterus gradually but rapidly diminishes till it regains the size and structure of the unimpregnated condition. During this change the enlarged muscular fibres undergo fatty degeneration and are said to become subsequently absorbed, while a new set of fibre-cells is developed. After the first pregnancy, however, the organ never regains its original virgin character. In those who have had children its weight usually remains from two to three ounces; its cavity is larger (fig. 611, C); the os externum is wider and more rounded, and its margins often puckered or fissured; the arteries continue much more tortuous, and its muscular fibres and layers remain more defined than in the virgin.

Changes from Age.—In the infant, the neck of the uterus is larger than the body; the fundus is not distinguished either by breadth or convexity of outline, and the cavity is remarkably narrow, and tapers out from the middle on both sides so as to present an approach to the two-horned form prevalent in animals. These parts afterwards enlarge gradually, until, at puberty, the pyriform figure of the womb is fully established (fig. 611, A.) The arbor vitæ is very distinct, and indeed at first reaches upward to the highest part of the cavity. The shape of the cavity of the body varies also in after life; but it remains comparatively narrow up to the age of puberty, and retains the same form to a great degree in all women who have borne no children (B). It is chiefly, therefore, in those who have been pregnant that its form is widely triangular (C).

From the gradual effects of more advanced age alone, independent of impregnation, the uterus shrinks, and becomes paler in colour, and harder in texture; its triangular form is lost; the body and neck become less distinguishable from each other; the orifices also become less characteristic.

Malformations.—The uterus is subject to numerous congenital malformations, especially in connection with abnormal conditions of the other genital organs. These will be referred to under Development. As a malformation affecting the uterus itself may here be mentioned the more or less double or divided state of the cavity, produced by the prolongation of a septum downwards into it from the fundus. This is sometimes only partial and confined to the upper part of the cavity; while in other instances it involves the whole cavity or also that of the cervix; and even extends through a part or the whole of the vagina.

THE FALLOPIAN TUBES.

These tubes may be considered as ducts of the ovaries (oviducts) and serve to convey the ovum from thence into the uterus. They are inclosed, as already stated, in the free margin of the broad ligaments, and are between three and four inches in length. Their inner or attached extremities, which proceed from the upper angles of the uterus, are narrow and cord-like (fig. 608, *od*): but they soon begin to enlarge, and proceeding outwards, one on each side, pursue an undulatory course, and at length, having attained the width of about a sixth of an inch or more (*i*), they bend backwards, inwards, and downwards towards the ovary. About an inch beyond this they terminate in an expanded extremity, the margin of which is divided deeply into a number of irregular processes named *fimbriæ* (*fi*); one of these, somewhat longer than the rest, is attached to the upper end of the corresponding ovary (fig. 603). The wide and fringed end of the Fallopian tube, or *trumpet*, as the term "tuba" literally signifies, is turned towards the ovary, and is named the *fimbriated extremity* (morsus diaboli). In the midst of these fimbriæ, which are arranged in a radiated manner, the tube itself opens by a round constricted orifice (fig. 603, 4), *ostium abdominale*, placed at the bottom of a sort of fissure leading from that fringe which is attached to the ovary. It is by this orifice that an ovum is received at the time of its liberation from the ovary, and is thence conveyed along the tube, which narrows very much towards its uterine extremity, and opens into the womb by a minute orifice, admitting only a fine bristle, and named *ostium uterinum*. The canal becomes gradually larger towards its abdominal orifice, where it is again somewhat contracted: hence the term *isthmus*, given by Henle to the uterine half, and *ampulla* to the outer half of the Fallopian tube. A second smaller fimbriated opening not unfrequently occurs at a short distance from the main one.

Beneath the external or peritoneal coat the walls of the tube contain, besides areolar tissue, plain muscular fibres, arranged in an external

longitudinal and an internal circular layer. The mucous membrane lining the tubes is thrown into longitudinal plicæ, which are broad and numerous in the wider part of the tube, and in the narrower part are broken up into very numerous arborescent processes: it is continuous, on the one hand, with the lining membrane of the uterus, and at the other end of the tube with the peritoneum; presenting an example of the direct continuity of a mucous and serous membrane, and making the peritoneal cavity in the female an exception to the ordinary rule of serous cavities, *i.e.*, of being perfectly closed to the exterior. The epithelium in the interior of the Fallopian tube is, like that of the uterus, columnar and ciliated; the inner surface of the fimbriæ is also provided with cilia, on their outer or serous surface it passes into the pavement epithelium of the peritoneal membrane. It does not appear that there are glands, as was at one time supposed, in the mucous membrane lining the Fallopian tubes.

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On the position and form of the uterus:—*Guyon*, Cavité de l'Utérus, &c., Journ. de la Physiol. II.; *J. Williams*, The Physiological Changes in the Position of the Uterus, 1873; *Braxton Hicks*, in Brit. Med. Journ. 1876; *B. S. Schultze*, in Arch. f. Gyn. IX. 1876, and Centralbl. f. Gyn. 1878; *Frankenhauser*, in Correspond.-bl. f. Schweitzer-arzte VI. 1876; *Fürst*, in Tagebl. d. 49. Versamml. Deutsch. Arzte, 1876; *E. Martin*, in Z. f. Geburtshülfe I. 1876; *Schröder*, in A. f. Gyn. IX. 1876; *H. Beigel*, Pathol. Anat. d. Steril., Braunsw., 1878; *Hach*, Diss., Dorpat, 1877; *Langerhans*, in A. f. Gyn. XIII. 1878; *His*, Ue. Prep. z. Situs Viscerum in A. f. Anat. 1878, and *Warker*, in Amer. Journ. of Obstet., 1878 (contains very complete literature); *D. B. Hart*, in Edinb. Med. Journ. XXIV. 1879; *Küstner*, in A. f. Gyn. XV.; *Cowan*, in Amer. Pract., 1879; *Kocks*, Lage d. Uterus, Bonn, 1880.

On the Fallopian tubes:—*Hennig*, in A. d. Heilk. XVIII. 1877, and Arch. f. Gyn. XIII. 1879.

THE OVARIES.

The **ovaries** are two somewhat flattened oval bodies, which are placed one on each side of the pelvis, enveloped in the posterior layer of the broad ligament of the uterus. The weight of each is from sixty to a hundred grains, and they usually measure about one inch and a half in length, three quarters of an inch in width, and nearly half an inch in thickness, but their size is variable. Each ovary is free on its two sides, also along one border, which has a convex outline; but it is attached to the broad ligament by the opposite border, which is straighter than the other, and along the line of its attachment the vessels and nerves enter (*hilus*). Its lower end is generally narrower than the upper, and is attached to the uterus by the ligament of the ovary. To its upper extremity is attached the ovarian fimbria of the Fallopian tube.

The exact position of the ovary is by no means uniform in different individuals, and opinions are much divided as to the condition which is to be regarded as

normal. According to Kölliker, the ovary is most frequently placed obliquely, having its long axis parallel to the external iliac vessels, its surfaces directed inwards and outwards, and its free border upwards and forwards. His, on the

Fig. 612.

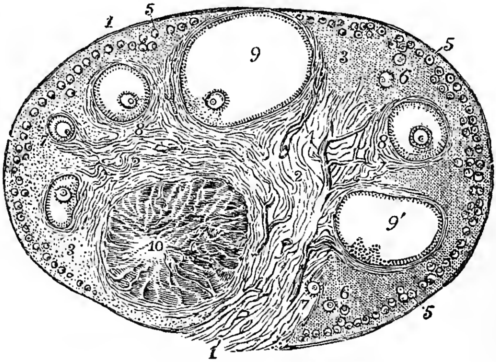

Fig. 612.—SECTION OF THE OVARY OF THE CAT (from Schrön). $\frac{6}{1}$

1, outer covering and free border of the ovary; 1′, attached border; 2, the central ovarian stroma, presenting a fibrous and vascular structure; 3, peripheral stroma; 4, blood-vessels; 5, Graafian follicles in their earliest stages lying near the surface; 6, 7, 8, more advanced follicles which are imbedded more deeply in the stroma; 9, an almost mature follicle containing the ovum in its deepest part; 9′, a follicle from which the ovum has accidentally escaped; 10, corpus luteum.

other hand, states that the ovary is naturally vertical, with its free border turned backwards. It frequently happens that the uterus is inclined somewhat to one side, and then the lower end of the opposite ovary is drawn inwards to a corresponding degree, so that the organ assumes a more transverse position

Fig 613.

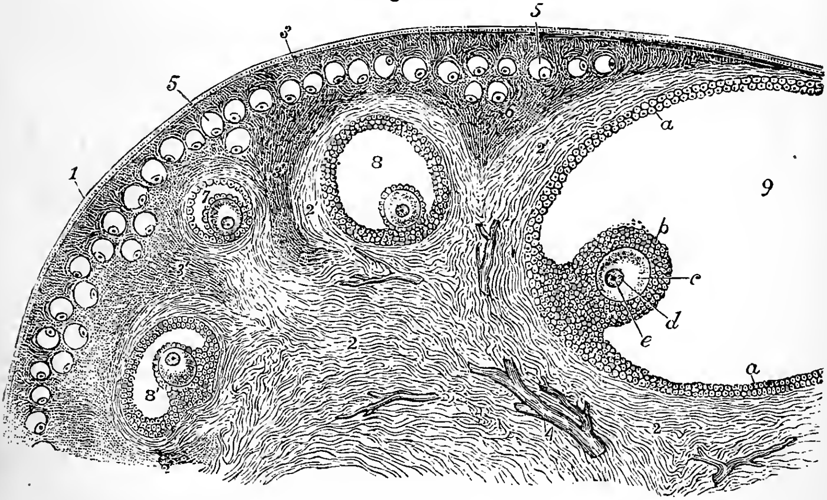

Fig. 613.—PORTION OF THE SECTION OF THE PREPARED CAT'S OVARY, REPRESENTED IN THE PRECEDING FIGURE, MORE HIGHLY MAGNIFIED (from Schrön).

1, epithelium and outer covering of the ovary; 2, fibrous stroma; 3, 3′, less fibrous, more superficial stroma; 4, blood-vessels; 5, small Graafian follicles near the surface; 6, one or two more deeply placed; 7, one farther developed, enclosed by a prolongation of the fibrous stroma; 8, a follicle farther advanced; 8′, another which is irregularly compressed; 9, part of the largest follicle; *a*, tunica granulosa; *b*, discus proligerus; *c*, ovum; *d*, germinal vesicle; *e*, germinal spot.

Structure of the ovary.—The ovary consists of stroma, composed of connective tissue with blood-vessels, nerves, and plain muscular fibres, and it has an outer epithelial covering, in which are embedded Graafian follicles containing ova.

Epithelium and stroma.—The external surface of the ovary is of a whitish colour, and in early life is comparatively smooth and even; but in later life it becomes more uneven and is marked by pits and scars. It is covered by an epithelium which differs from that of the peritoneum in being composed of pyriform or columnar cells: and the surface has a dull appearance as compared with the shining smoothness of the serous membrane. A distinct line of demarcation exists around the attachment of the ovary, where the two kinds of epithelium pass into each other. This ovarian epithelium is the remains of the *germ-epithelium* from which the ova, and probably the other cells within the Graafian follicles have been developed in the embryo. Here and there are occasionally to be seen amongst the ordinary epithelium-cells, others which are much enlarged and of a spherical form. These are primitive ova, similar to those from which the permanent ova are formed in the fœtus and young subject, and it is probable that even in the adult the formation of ova from cells of the germ-epithelium may proceed to some extent.

Within the epithelium a firm layer of fibrous tissue encloses all the deeper parts. This has been compared to the dense fibrous covering of the testicle, and thence named tunica albuginea ovarii, but without sufficient reason, for it is not a distinct tunic, and is in fact no more than a condensed part of the ovarian stroma.

The *stroma* is chiefly composed of a fine connective tissue, in which the cells, many of which are spindle-shaped, are remarkably abundant and distinct. Besides the spindle-shaped cells, others are met with which closely resemble the interstitial cells of the intertubular substance of the testis. Like these, they have a polyhedral or irregular shape and often a yellowish colour, and they are chiefly found accompanying the blood-vessels, although in older ovaries they may be very extensively diffused throughout the stroma. The stroma also contains elastic tissue, and is permeated by blood-vessels, which are large towards the hilus and in the centre of the ovary where the tissue is more fibrous, and become gradually smaller towards the surface. Along these blood-vessels in the deeper part of the ovary bands of muscular fibres run, having entered from the broad ligament; but it is uncertain whether they extend into the more superficial parts of the ovarian stroma. According to some authorities the spindle-shaped cells which characterize the ovarian stroma are also of muscular nature.

There is a general radial disposition of the bands of stroma from the hilus towards the surface.

Graafian Follicles.—Immediately under the superficial covering of the ovary there is a layer of stroma somewhat different from the deeper parts, and which is so uniformly spread over the organ as to have received the name of cortical layer. This is particularly obvious in the ovaries of some animals (fig. 612, 5) and of young children, in whom this layer is comparatively thick, and to the naked eye its appearance is granular from the accumulation in it of an immense number of closely set small vesicles, constituting the early condition of the ovarian or Graafian follicles with their contained ova. Embedded more deeply in the substance of the ovary are seen other larger and less numerous follicles

of varying size, the largest being also the most deeply seated. The very largest, however, which are approaching maturity, eventually reach the surface again, owing to their being gradually more and more distended with fluid, and may there be seen projecting somewhat, in the form of clear vesicles, from one-twentieth to one-sixth of an inch in diameter. When these are punctured or ruptured a drop of clear fluid (*liquor folliculi*) escapes, carrying with it the minute ovum surrounded by an accumulation of the epithelium-cells of the follicle, known as the *discus proligerus*. Rupture of a Graafian vesicle, or it may be of more than one, occurs in healthy females at or before every

Fig. 614.

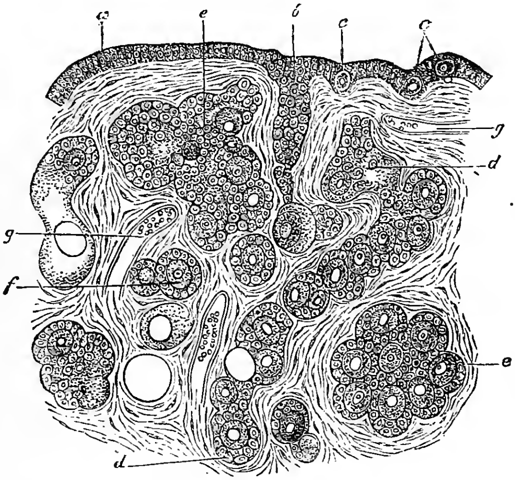

Fig. 614.—Section of the ovary of a newly-born child. Highly magnified (Waldeyer).

a, Ovarian or germinal epithelium ; *b*, formation of an ovarian tube ; *c*, *c*, primordial ova lying in the germ-epithelium ; *d*, *d*, longer tube becoming constricted so as to form nests of cells ; *e*, *e*, larger nests ; *f*, distinctly formed follicle with ovum and epithelium ; *g*, *g*, blood-vessels.

successive menstrual period. After the discharge of its contents, the empty and collapsed Graafian follicle becomes filled with a peculiarly reddish-yellow tissue and constitutes a body termed *corpus luteum*. Should pregnancy occur, this body undergoes a considerable development, which is maintained during the greater part of the time of utero-gestation. But in the unimpregnated female the corpus luteum begins to retrograde within ten or twelve days after its commencement, and afterwards shrinks and ultimately disappears. Other follicles, especially before and after the child-bearing period, may after advancing to a certain stage of development undergo a retrograde metamorphosis, their contents becoming broken up and liquefied and their walls collapsed and converted into a non-vascular homogeneous membrane. Follicles in this condition are not at all unfrequent in the deeper parts of the ovary (fig. 615, *k*).

In addition to Graafian follicles in various stages of development and retrogression, there may also occasionally be seen in sections of the adult ovary and constantly in that of the young subject, cords or tubes composed of rounded

or polyhedral cells, sometimes with developing ova imbedded amongst the other cells. These cords may be in continuity with the germinal epithelium or they may be altogether cut off from it. Others occur which are partially constricted into rounded nests of cells by growth of the stroma across the cords, and similar nests or groups are found entirely separated, and with or without a developing ovum in the centre. It is from these nests of cells that the Graafian follicles become developed, but the mode in which this occurs and also the changes which the primitive ova undergo in becoming converted into the permanent ova, will be described in the Chapter on Development.

Structure of the Graafian follicles.—The smallest Graafian follicles have no proper wall. They consist merely of a single layer of imbricated flattened cells, immediately investing the contained ovum. In section, the cells look spindle-shaped in the human subject, and not very unlike the cells of the ovarian stroma, so that they were thought by Foulis to be derived from those cells; but the observations of Balfour and others upon the lower animals tend to confirm the view which was first stated by Waldeyer that, like the ova themselves, these epithelium-cells of the follicles are originally derived from the germinal epithelium. These smallest follicles are very numerous, especially in the young subject; indeed, it has been computed that in the ovaries of a female child at birth there cannot be fewer than 70,000 of them. If this is the case, a large proportion must degenerate and disappear without coming to maturity. Their size is about $\frac{1}{100}$th of an inch.

In follicles which are a little larger, and situated somewhat more deeply in the stroma, the epithelium-cells, although still in a single layer, are no longer flattened but cubical; a *membrana propria* or basement membrane can be detected, and the layer of stroma next to the follicle is beginning to be somewhat differentiated from the rest so as to form a special fibrous wall to the follicle. In others again a second layer of cells is beginning to be formed or may be found entirely formed within the first, and of the two layers thus produced, one immediately invests the ovum, and the other lines the wall of the follicle. The former is the beginning of the *discus proligerus*, and the latter of the *membrana granulosa*. The cells of both layers soon become columnar.

In most animals the second or inner layer of cells appears to be formed by division of the cells of the first formed layer, but in the rabbit the appearances which are observed appear to justify the assumption that the inner layer is formed at the expense of the peripheral part of the ovum itself (E.A.S.).

In follicles which are still larger, fluid is seen to be accumulated between the two layers of cells, and thus to distend the follicle. This collection of fluid is absent at one part, generally that which is directed away from the surface of the ovary, so that here the cells which surround the ovum are in continuity with those which line the follicle, and the ovum is thus in a manner attached at this place to the wall of the follicle (see fig. 613). In the largest follicles the chief difference in the contents of the follicle consists in the far greater accumulation of the liquor folliculi, and in the multiplication of the epithelium-cells—both those which line the follicle (membrana granulosa) and those which invest the ovum (discus proligerus)—so that each of these parts consists, in large follicles, of several layers of cells, mostly rounded or irregular, but columnar next the wall of the follicle and the exterior of the ovum respectively.

The larger follicles have a very distinct wall, which is continuous with and derived from the stroma of the ovary, and is separable into two

parts, an inner containing the ramifications of the capillary blood-vessels, which are abundantly distributed to the larger follicles, but nowhere penetrate amongst the epithelium cells; and an outer part more fibrous, in

Fig. 615.

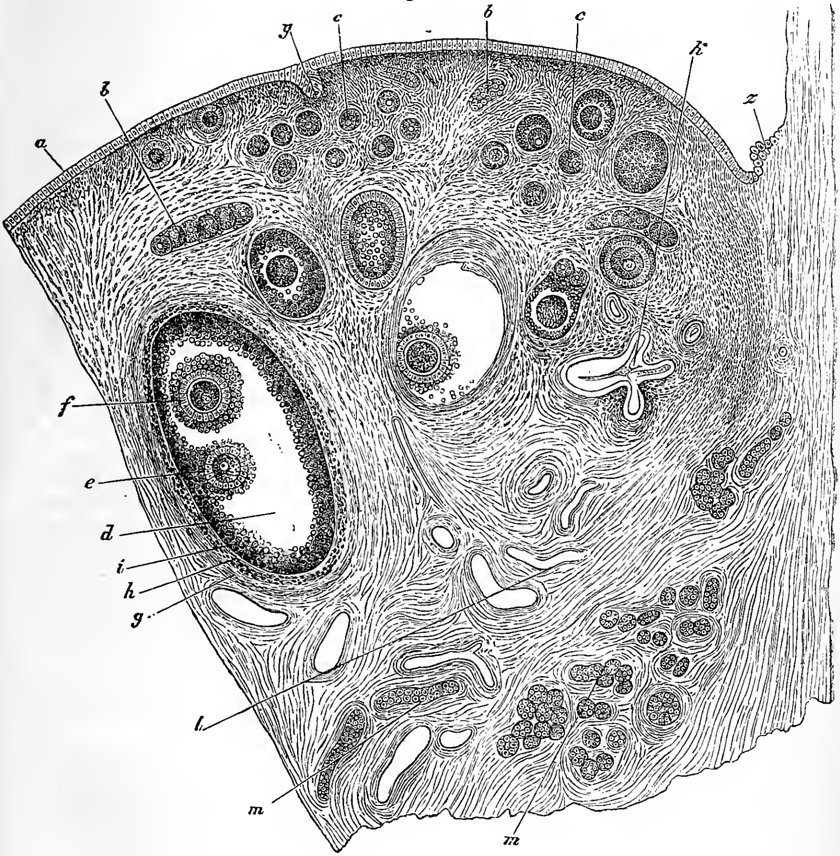

Fig. 615.—Section of the ovary of an adult bitch (Waldeyer). $\frac{15}{1}$

a, germ-epithelium; *b*, egg-tubes; *c*, *c*, small follicles; *d*, more advanced follicle; *e*, discus proligerus and ovum; *f*, second ovum in the same follicle (this occurs but rarely); *g*, outer tunic of the follicle; *h*, inner tunic; *i*, membrana granulosa; *k*, collapsed retrograded follicle; *l*, blood-vessels; *m*, *m*, longitudinal and transverse sections of tubes of the parovarium; *y*, involuted portion of the germ-epithelium of the surface; *z*, place of the transition from peritoneal to germinal or ovarian epithelium.

which the larger branches of the blood-vessels of the follicle run. In both layers of the follicular wall, the cells are similar to those of the general stroma, interstitial cells occurring abundantly; but it is uncertain whether there are any cells present of the nature of muscular fibres. The smaller blood-vessels running round the follicle from below, and minutely subdivided on its inner surface, converge towards a point near the middle of the most projecting part, called the *stigma*. This marks the spot where the rupture of the vesicle ultimately occurs, when fully matured.

Each Graafian follicle usually contains only a single ovum; but occasionally, though seldom, two ova, and very rarely three, have been observed in the same follicle. The structure of the ovum will be described in the Chapter on Development.

Structure of the corpora lutea.—The corpora lutea are produced after the rupture of the Graafian follicles and the escape of their contents by what may perhaps be most correctly described as a process of hypertrophy which the walls of the empty follicles undergo, without the follicle itself submitting to a corresponding amount of enlargement. The result is that the hypertrophied follicular wall is thrown into plaits or folds which as they increase in extent occupy more and more of the cavity of the empty follicle, until this has become entirely filled. The hypertrophy appears to be chiefly the result of the proliferation of the polyhedral interstitial stroma-cells, which as already stated occur in the wall of the follicle in abundance, and there is in addition a considerable development of blood-vessels, which run, accompanied by fibrous tissue, into the folds into which the wall of the follicle is thrown, giving off capillaries which ramify abundantly in the folded wall. Meanwhile the irregular cleft-like space which now alone represents the cavity of the follicle, as well as the opening resulting from the rupture of the follicle and by which its cavity communicated with the surface, have become occupied by a sort of cicatricial fibrous tissue, which constitutes a sort of hilus for the follicle. To this central fibrous band the strands of fibrous tissue which accompany the blood-vessels in the folds of the hypertrophied follicular wall converge. And at the same time the plaited disposition of the wall becomes in great measure obscured, so that a section of a corpus luteum, when advanced in development, exhibits a fibrous framework having a somewhat radial disposition, with the intervals between the radiating trabeculæ occupied by a tissue which is almost wholly composed of the yellowish interstitial stroma-cells. Amongst these cells are numerous cleft-like lymphatic spaces, and except for the fact that capillary blood-vessels also ramify between the yellowish cells, the structural appearances are not unlike those which are met with in the cortical part of the suprarenal capsule.

The corpus luteum is at first marked off from the surrounding ovarian stroma, but after a time its limits are less well defined, at the same time that many of its cells wander into the neighbouring parts of the stroma, into which it may be said gradually to merge and in this way to disappear. The result is that, as age advances, the stroma of the ovaries becomes gradually more and more pervaded with interstitial cells.

It is asserted by some that the cells of the membrana granulosa take part in the formation of the corpus luteum, but it is more probable that they become detached and extruded shortly after the escape of the ovum. The characters of the cells of the yellow body, the vascularization of its tissue, and its subsequent blending with the general ovarial stroma, are all facts which point to the derivation of the corpus luteum from the wall of the follicle rather than from the epithelium which forms the membrana granulosa.

Vessels and nerves of the ovaries and Fallopian tubes.—The ovaries are most directly supplied by the *ovarian arteries*, analogous to the spermatic in the male, which anastomose freely by an internal branch with the termination of the uterine arteries. Sometimes this anastomotic branch is so large that the ovary seems to be supplied almost entirely by the uterine artery. The ovarian artery always sends numerous branches to the Fallopian tube. The smaller arteries penetrate the ovary along its attached border, pierce the proper coat, and run in flexuous parallel lines through its substance. The *veins* correspond, forming a plexus near the ovary named the *pampiniform plexus*. The *nerves* are derived from the *ovarian plexus*; and also from the uterine nerves, which invariably send offsets to the Fallopian tubes.

Parovarium.—The organ so named by Kobelt, or the Organ of Rosenmüller, its first describer, is a structure which can usually be brought plainly into view by holding against the light the fold of peritoneum between the ovary and Fallopian tube (see fig. 608, *po*). It consists of a group of scattered tubules lying

transversely between the Fallopian tube and ovary, lined with epithelium, but having no external openings. The tubules converge towards their ovarian end, but remain separate there, while at the other they are more or less distinctly united by a longitudinal tube which is sometimes of considerable size, and prolonged for some distance downwards in the broad ligament. Its more developed form in some animals, as the cow and pig, constitutes the duct of Gaertner. The origin of this vestige of a fœtal structure will be more fully referred to under Development. Here it is sufficient to state that it corresponds essentially to the epididymis of the male. Vestiges of the organ of Giraldès are also sometimes to be detected in the adult female, in the shape of tubular remnants, situated in the broad ligament nearer to the uterus than the parovarium.

Recent Literature.—Of the Ovary :—*Waldeyer*, Eierstock u. Ei, Leipzig, 1870, and Art. in Stricker's Handbook, 1871 ; *Romiti*, in Arch. f. mikr. Anat. X. 1873 ; *Kölliker*, in Wurzb. Verhandl., 1874 ; *Foulis*, in Trans. R. S. Edinb., 1874. and J. of Anat., XIII., 1879 ; *Call & Exner*, in Wien. Sitzungsb., 1874 (Graaf. foll. and corp. lut.) ; *Slaviansky*, in Arch. de physiol., 1874 (str. and retrogr. of Graaf. foll.) and Annales de Gyn., IX. 1878 ; *Exner & Buckel*, in Wien. Sitzungsb., 1874 (lymphatics) ; *Born*, in A. f. Anat., 1874 (ovary of horse) ; *Elischer*, in Med. Centralbl., 1876 (nerves) ; *de Sinéty*, in Comptes rend. LXXXV., 1877 ; *Beulin*, Diss., Königsb. 1877 (corp. lut.) ; *H. Beigel*, in Arch. f. Gyn., XIII. (corp. lut.) ; *Kisch*, in Arch. f. Gyn., XII. 1878 (changes in Graaf. foll. in age) ; *Balfour*, in Quart. Micr. Journ. XVIII., 1878 ; *Wagener*, in Arch. f. Anat., 1879 ; *Paladino*, in Gior. intern. d. sci. med., 1879 and 1880 (corp. lut.) ; *McLeod*, in Arch. de biol., I. 1880 ; *v. Beneden*, in the same ; *Schäfer*, in Proc. R. S. XXX., 1880 ; *v. Brunn*, in Gött. Nachr., 1880 (retrogr. of ova) ; *Cadiat*, in Journ. de l'anat., 1881 ; *Schulin*, in Arch. f. mikr. Anat. 1881 ; *His*, Lage der Eierstöcke, Arch. f. Anat., 1881 ; *Kölliker*, Lage d. weibl. inneren Geschlechtsorgane, Bonn, 1882.

On the Discharge of Ova :—*J. Williams*, in Pr. R. S. XXIII., 1874 ; *Hennig*, in Leipzig Sitzungsb., 1878 ; *Galabin*, in Obstetr. Journ., 1879 ; *Pinner*, in Arch. f. (Anat. u.) Physiol., 1880 ; *Leopold*, in Arch. f. Gyn., XVI., 1880.

MAMMARY GLANDS.

The mammary glands (mammæ), which yield the milk in the female, are accessory parts to the reproductive system. They give a name to a large class of animals (Mammalia), which are distinguished by the possession of these organs. When fully developed in the human female, they form, together with the integuments and a considerable quantity of fat, two rounded eminences (the breasts) placed one at each side on the front of the thorax. These extend from the third to the sixth or seventh rib, and from the side of the sternum to the axilla. A little below the centre of each breast, on a level with the fourth rib, or slightly lower, projects a small conical body named the *nipple* (mammilla), which points somewhat outwards and upwards. The surface of the nipple is dark, and around it there is a coloured circle or *areola*, within which the skin is also of a darker tinge than elsewhere. In the virgin, these parts are of a rosy pink colour, differing somewhat according to the complexion of the individual, but they are always darker in women who have borne children. Even in the second month of the first pregnancy, the areola begins to enlarge and acquire a darker tinge ; these changes go on increasing as gestation advances, and are regarded as signs to be relied on in judging of suspected pregnancy. After lactation is over, the dark colour subsides, but never entirely disappears. The skin of the nipple is marked with many wrinkles, and is covered with papillæ ; besides this, it is perforated at the tip by numerous foramina, which are the openings of the lactiferous ducts : and near its base, as well as upon the surface of the areola, there are scattered rounded elevations, which are caused by the presence of little glands with branched

ducts, four or five of which open on each elevation. The tissue of the nipple contains a large number of vessels, together with much plain muscular tissue, and its papillæ are highly sensitive; it becomes firmer and more projecting from mechanical excitement,—a change mainly caused by contraction of the muscular fibres, which form concentric circles round the base of the nipple, and radiating bands running from base to apex.

The base of the mammary gland is flattened, or slightly concave, and somewhat oval, with its longest diameter directed upwards and out-

Fig. 616.

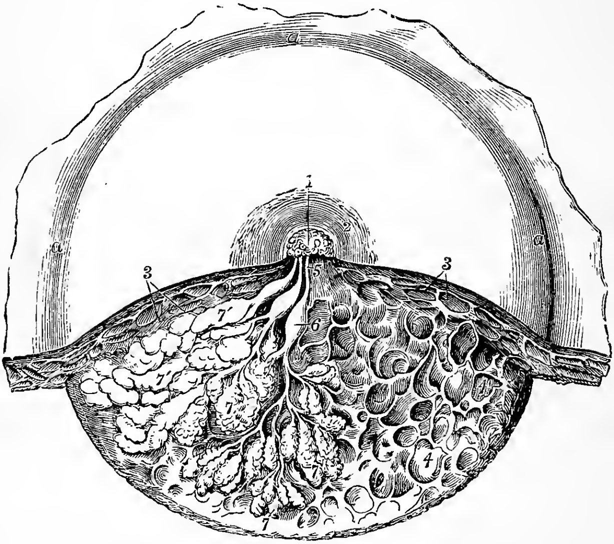

Fig. 616.—Dissection of the lower half of the female mamma during the period of lactation (from Luschka). $\frac{2}{3}$

a, *a*, *a*, undissected part of the mamma; 1, the mammilla; 2, areola; 3, subcutaneous masses of fat; 4, loculi in the connective tissue which supports the glandular substance; 5, three lactiferous ducts passing towards the mammilla where they open; 6, one of the sinuses or ampullæ; 7, some of the glandular lobules which have been unravelled; 7′, others massed together.

wards towards the axilla. The gland lies in connective tissue continuous with the superficial fascia, its base resting on the pectoral muscle, and separated from it by a layer of firm areolar tissue continuous with the deep fascia. The thickest part of the gland is near the centre, opposite the nipple.

On the surface, and penetrating also between the lobes, there is a large quantity of fat, which mainly gives the full and smoothly rounded form to the gland. This fat is of a firm consistence and bright yellow colour, and is subdivided into lobules by partitions of connective tissue. It is entirely absent from the nipple and areola.

Structure.—The glandular substance of the mamma consists of numerous distinct lobes held together by firm intervening fibrous or areolar tissue, and having adipose tissue penetrating between them. Each of these lobes is provided with an excretory duct, and is subdivided

into smaller lobes, and these again into smaller and smaller lobules, which are flattened or polyhedral, and are united by areolar tissue, blood-vessels, and ducts. The interlobular tissue contains numerous plasma-cells. The substance of the lobules is of a pale reddish cream-colour, contrasting with the adjacent fat, and is rather firm. The excretory ducts, named the *galactophorous ducts*, are from fifteen to twenty in number; they converge towards the areola, beneath which they become considerably dilated, especially during lactation, so as to form *ampullæ* or *sinuses* $\frac{1}{6}$th to $\frac{1}{4}$th of an inch wide, which serve as small temporary reservoirs for the milk. At the base of the nipple all these ducts, again reduced in size, are assembled together, those in the centre being the largest, and then proceed, side by side, surrounded by areolar tissue and vessels, and without com-

Fig. 617.

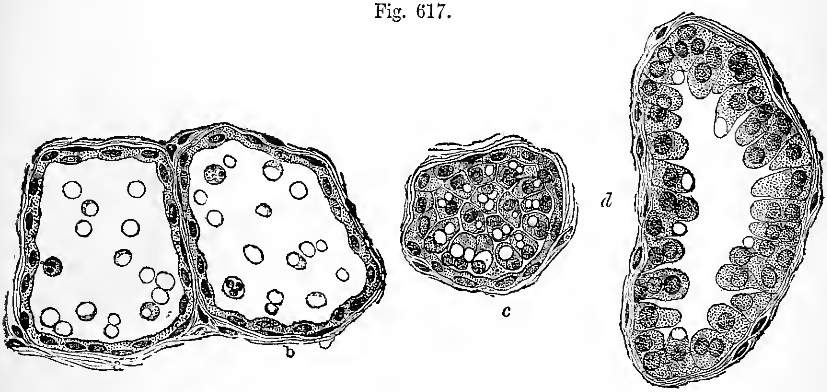

Fig. 617.—Alveoli of the mammary gland of the bitch under different conditions of activity (Heidenhain).

a, b, section through the middle of two alveoli at the commencement of lactation, the epithelium cells being seen in profile; *c,* part of the wall of an alveolus in a similar condition with the epithelium cells seen flat; *d,* an alveolus in full secretory activity.

municating with each other, to the summit of the mamilla, where they open by separate orifices; these orifices are seated in little depressions, and are smaller than the ducts. The walls of the ducts are composed of areolar tissue, with longitudinal and circular elastic fibres. Both the terminal vesicles and the ducts are lined with a simple layer of epithelium, which passes into stratified near the external openings on the nipple.

The membrana propria of the alveoli appears to consist of a homogeneous membrane having stellæ and anastomosing cells upon its inner surface next to the epithelium.

The epithelium differs in its appearance according to the state of activity of the gland. When entirely inactive the alveoli are very small, and the epithelium cells small and granular. At the commencement of lactation the alveoli enlarge and become distended with clear secretion (fig. 617, *a, b*); the cells are flattened out against the membrana propria and contain fat globules of varying size and in the fluid contents of the alveoli besides similar fat globules, some of which have a partial surrounding of protoplasm, a few uni- or multi-nucleated granular cells are seen. During full activity the cells become cubical or even columnar, but are irregular in size and exhibit indications of division and of budding off

into the interior of the alveoli (fig. 617, *d*). By the breaking down of the cells which have thus become free in the alveoli the constituents of the milk appear to be formed, the fat globules which were present within the cells becoming suspended in the fluid of the alveoli as milk globules, and the albuminous constituents of the cells becoming dissolved and forming the casein and other proteid substances of the milk.

There is a rich network of blood-capillaries investing the alveoli, and these are also surrounded by lymph-sinuses like those met with in other racemose glands.

Difference according to sex.—The mamma begins to be formed as early as the fourth month of fœtal life, but its subsequent growth is comparatively tardy. At the third or fourth year of infancy, there is little or no difference in male and female children. The fuller development of the gland in the female occurs only towards puberty. It is probable that during the later periods of pregnancy, not only do the alveoli increase in size, but new alveoli may bud laterally from the pre-existing ones, and that after lactation some of the alveoli may become atrophied and disappear.

In the adult male the mammary gland and all its parts exist, but quite in a rudimentary state, the gland itself measuring only from half to three quarters of an inch across, and $\frac{1}{6}$th of an inch thick, instead of four inches and a half wide, and one and a half thick, as in the female. Occasionally the male mamma, especially in young subjects, enlarges and gives out a thin watery fluid; and, in rare cases, it has secreted milk.

Blood-vessels and Nerves.—The **arteries** which supply the mammary glands are the *long thoracic* and some other branches of the axillary artery, the *internal mammary*, and the subjacent *intercostals*. The **veins** have the same denomination. Haller described a sort of anastomotic venous circle surrounding the base of the nipple as the *circulus venosus*. The **nerves** proceed from the anterior and middle *intercostal* cutaneous branches.

Varieties.—Two or even three nipples have been found on one gland. An additional mamma is sometimes met with, and even four or five have been observed to co-exist; the supernumerary glands being most frequently near the ordinary pair, but sometimes in a distant part of the body, as the axilla, thigh, or back.

Milk.—The milk is characterized by containing an immense number of fat-globules of varying size but averaging from $\frac{1}{12000}$th to $\frac{1}{5000}$th of an inch in diameter. They appear to be coated with an exceedingly thin investment of albuminous substance, probably casein, which prevents them from running together into larger drops, but when this is dissolved by the addition of an acid, they readily blend with one another. Rarely there is a more distinct, entire or partial, envelope of granular substance, occasionally containing a nucleus, and free nuclei have also been described as existing to a small extent in the milk.

The mammary gland before and during the first two or three days after parturition yields a small amount of a turbid fluid termed the *colostrum*. This contains besides milk-globules single and in groups, amœboid cells, containing

Fig. 618.

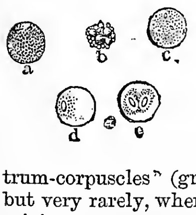

Fig. 618.—Constituents of the colostrum (Heidenhain).

a, *b*, colostrum-corpuscles with fine and coarse fat-globules respectively; *c*, *d*, *e*, pale cells devoid of fat globules.

small or large fat-globules, either closely packed within the cell, or but few in number, or even absent altogether, and in the latter case permitting the nucleus to be visible (fig. 618). These amœboid cells are known as the "colostrum-corpuscles" (granular corpuscles of Donné): they occur either not at all or but very rarely, when the gland is in full activity. It is uncertain whether they originate as separated epithelium-cells of the alveoli, or whether they are emigrated white corpuscles.

Recent Literature.—On the structure of the mammæ :—*Langer*, in Stricker's Handb., 1871; *v. Brunn*, in Gött. Nachr., 1874 (interstitial tissue) ; *Coyne*, Soc. d. biol., 1874 (lymphatic sinuses) ; *Winkler*, in Dresden Jahresb., 1874, and A. f. Gynäk. XI., 1877 ; *Kolessnikow*, in Virch. Arch., 1877 ; *Schmid*, Z. Lehre v. d. Milchsecr., Wurzb., 1877 ; *de Sinéty*, in Gaz. méd., 1877 ; *Creighton*, Privy Council Reports, 1875, and Jour. of Anat., 1876 ; *Kölliker*, in Wurzb. Verhandl., XIV., 1879 ; *Rauber*, Ursprung d. Milch, Leipzig, 1879 ; *Partsch*, Diss., Breslau, 1880 ; *Sorgius*, Diss., Strasburg, 1880 (lymphatics); *Heidenhain*, Article "Milch-Absonderung," in Hermann's Handb., 1880.

On the male mamma :—*W. Gruber*, St. Petersb. Mem., 1866.

On supernumerary nipples and mammæ :—*Gegenbaur*, in Jena Zeitschr., VII. ; *J. Mitchell Bruce*, in J. of Anat. & Phys. XIII., 1879.

On the microscopic elements of the milk :—*Schwalbe*, in Arch. f. mikr. Anat., VIII. 1872 ; *de Sinéty*, in Arch. de physiol., 1874 ; *Fleischmann*, "Das Molkereiwesen," Braunschw., 1875 ; *Schmid*, Op. cit., 1877 ; *Bouchut*, in Compt. rend., 1877 (numeration of globules) ; *Heidenhain*, Op. cit., 1880.

THE PERITONEUM.

The abdominal viscera having been described, as well as the disposition of the peritoneum in relation to each of them, it remains to give an account of that membrane in its whole extent, and to trace its continuity over the various parts which it lines or covers.

After lining the anterior wall of the abdomen, the peritoneum passes round on each side to the lumbar region, where it meets with the right and left portions of the large intestine. On the right side it completely invests the lower rounded end of the cæcum with the vermiform appendix ; but the rest of the cæcum it covers only before and on the sides, a part of the bowel behind, of variable extent, being immediately adjacent to the iliac fascia, except in rare instances where the membrane goes entirely round and forms a mesocæcum. It is disposed in a similar manner on the ascending colon, which is in immediate apposition with the abdominal wall ; although here, too, the investment may be complete with a resulting right mesocolon.

Leaving the right colon, the peritoneum gives a scanty covering to the lower part of the anterior face of the right kidney and adjoining third portion of the duodenum where that intestine comes down from behind the transverse mesocolon ; lower down it continues over muscles and vessels to the root of the mesentery, proceeds forwards to form the right layer of that process, passes round the jejunum and ileum, affording them their peritoneal coat, and returns back to the vertebræ, thus completing the mesentery on the left side. The membrane now passes in front of the lower portion of the left kidney, to the left colon, which it invests much in the same manner as the right, and is then continued over the lateral wall on the left side to the front again, thus completing a horizontal circle round the abdomen. Where the colon forms its sigmoid flexure it is completely invested by peritoneum, which attaches it by a comparatively free and moveable sigmoid mesocolon to the fascia of the left iliac fossa.

From this part, and from the lower end of the mesentery the peritoneum is continued into the pelvis. It there invests the upper part of the rectum completely, forming a mesorectum behind. Lower down the membrane gradually quits the intestine, first behind, then at the sides, and finally in front, whence it is reflected on the base and upper part of the bladder in the male, and forms here the *recto-vesical pouch*, the mouth of which is bounded by a crescentic fold on each side, named *plica semilunaris*. From the apex of the bladder the peritoneum passes to the

back of the recti muscles. Here it covers the remains of the urachus

Fig. 619.

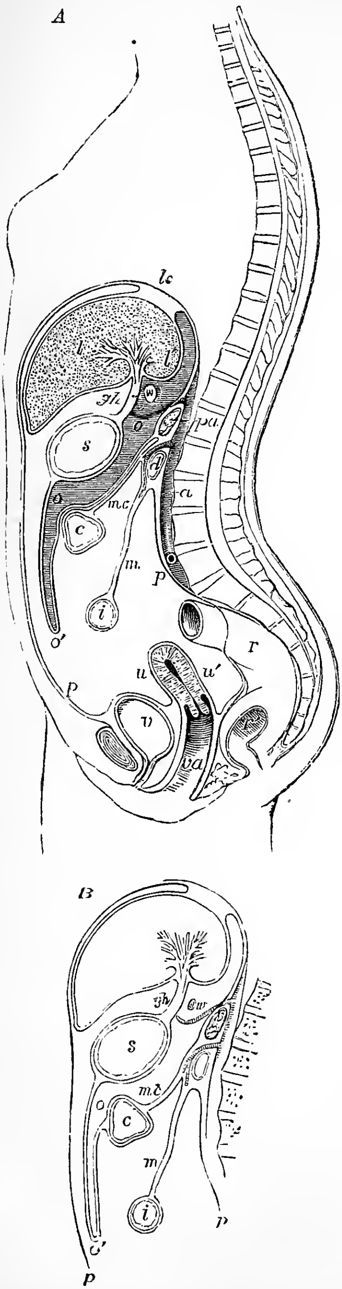

Fig. 619, A.—Diagrammatic outline of a supposed section of the body, showing the inflections of the peritoneum in the female (Allen Thomson). $\frac{1}{6}$

The upper part of the section is a little to the right of the mesial plane of the body, through the quadrate and Spigelian lobes of the liver below, it is supposed to be mesial: *l c*, placed above the diaphragm opposite to the coronary ligament of the liver; *l*, liver; *l'*, lobe of Spiegel; *s*, stomach; *c*, transverse colon; *i*, small intestine; *pa*, pancreas; *a*, aorta; *d*, duodenum; *v*, urinary bladder; *u*, uterus; *r*, rectum; *r'*, its lower part opened; *v a*, vagina; *p*, *p*, the parietal peritoneum lining the front and back of the abdominal cavity; the line representing the inflections of the greater sac of the peritoneum will be traced from the neighbourhood of *l c*, where it passes from the diaphragm to the upper surface of the liver, over the upper and lower surfaces of that organ, in the front of *g h*, the gastro-hepatic omentum, over the front of the stomach, down to *o'*, the outer layer of the great omentum; thence it passes back to the vicinity of the pancreas, and descends again as the upper layer of the transverse mesocolon; after enclosing the colon it returns on the lower surface of the transverse mesocolon, *m c*, to the root of the mesentery, *m*; it now forms the mesentery and encloses the small intestine, returning to the posterior wall of the abdomen, whence it passes over the rectum, *r*, descends into the recto-vaginal pouch, *u'*, covers the back and front of the uterus and the bladder partially, and regains the anterior abdominal wall above the pubis. In connection with the lesser sac of the peritoneum, *w* marks the position of the foramen of Winslow as if seen beyond the section; the lesser sac, with the cavity of the omentum, is shaded with horizontal lines, and is marked *o o*: round this space the line of the peritoneum may be traced from the diaphragm over the lobe of Spiegel, to the back of the gastro-hepatic omentum, thence behind the stomach and down into the great omentum; it then ascends to the pancreas, which it covers, and thence reaches again the diaphragm.

B is a sketch of part of a section similar to that of A, but showing the view more commonly taken, according to which the two layers of the mesocolon are continuous with the posterior pair of the layers of the great omentum.

in the median line, and the obliterated hypogastric artery on each side, which as it passes

from the bladder to the abdominal wall raises the peritoneum into a well-marked fold, separating two shallow pits named *internal and external inguinal pouches* (more fully described with the special anatomy of the groin). In the female the peritoneum passes from the rectum to the upper part of the vagina, and over the posterior and anterior surfaces of the uterus, whence it goes to the bladder. The *recto-vaginal pouch* (pouch of Douglas), like the recto-vesical, is bounded above by its semilunar folds, and the uterine peritoneum forms at the sides the broad ligaments of the uterus, along the upper border of which the Fallopian tubes receive from it a serous covering ; but at their fimbriated openings the peritoneum is continuous with the mucous membrane lining the tubes.

The peritoneum, on being traced to the upper part of the abdomen, is found to line the vault of the diaphragm, adhering moderately to the muscular and firmly to the tendinous part, and continuing down behind as far as the hinder surface of the liver and the œsophageal opening. It then passes forwards on to the liver, forming the falciform, coronary, and lateral ligaments of that organ, already specially described.

Turning round the anterior border it passes back on the under surface ; but, after covering the quadrate lobe, and arriving at the transverse fissure, it meets with a peritoneal layer from behind, and in association with it, stretches from the liver to the stomach, to form the lesser omentum, as will be presently explained. To the right of this part it invests the gall-bladder, more or less completely, and the under surface of the right lobe of the liver, covers anteriorly the adjacent part of the duodenum, and passes to the upper end of the right kidney, forming here a slight fold, named *hepato-renal ligament.* It then invests the hepatic flexure of the colon, and reaches the right colon, on which it has been already traced. To the left of the longitudinal fissure the peritoneum invests the whole of the left lobe of the liver, and stretches out as the long left lateral ligament above and beyond the œsophageal opening. It then passes down over that opening and covers the front and left side of the gullet, spreads over the left end of the stomach, where it passes off to invest the spleen, forming a duplicature named the *gastro-splenic ligament*, or *gastro-splenic omentum*, for it is connected below with the great omentum, and often reckoned as a part of it. When the membrane passes from the diaphragm to the stomach it forms a small duplicature to the left of the œsophagus, named the *gastro-phrenic ligament ;* it extends also as a generally stout and well marked fold (the *costo-* or *phreno-colic ligament*) from the diaphragm opposite the tenth and eleventh ribs to the splenic flexure of the colon, then passes over the splenic flexure, and reaches the left kidney and descending colon, where it has been already described.

Omenta.—The arrangement of the remaining part of the peritoneum —that between the stomach, liver, and transverse colon—is somewhat complex, in consequence of the membrane forming in this situation a second and smaller sac, which communicates towards the right with the general cavity by a narrow throat, named the *foramen of Winslow.* This passage, which readily admits a finger, is situate behind the bundle of hepatic vessels which stretches between the liver and duodenum ; behind the orifice is the vena cava ; above is the caudate lobe of the liver ; and its lower boundary is formed by the duodenum and a curve of the hepatic artery. From this opening the lesser sac spreads out to the left

behind the general or main sac of the peritoneum. It covers a part of the posterior abdominal wall, but in front and below it is applied to the back of the main sac, to which it adheres except where the stomach is interposed. Moreover, it indents, as it were, the back of the main sac, and between the stomach and colon protrudes into it in form of a great pouch—the bag of the omentum,—which thus has a double coat, formed by the apposition of the membranes of both sacs. To trace this arrangement more particularly : suppose a finger pushed into the foramen of Winslow, and the thumb brought to meet it from before, to the left of the hepatic vessels ; the membrane held between is double ; its anterior layer (from the greater sac), turns round the hepatic vessels into the foramen, and then belongs to the lesser sac. The double membrane, so constituted, is the lesser or hepato-gastric omentum. From the point

Fig. 620.

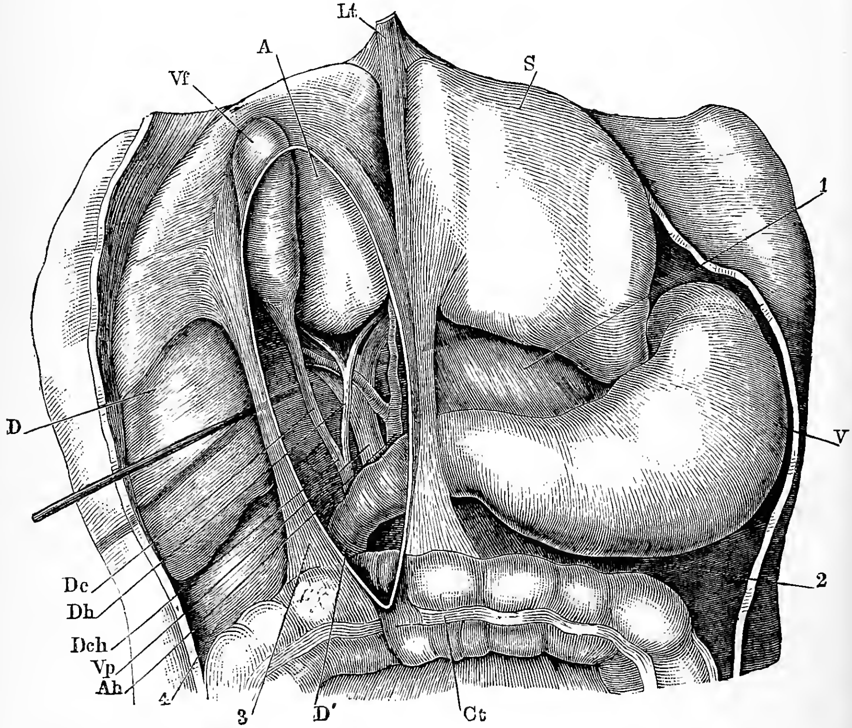

Fig. 620.—FRONT VIEW OF THE VISCERA OF THE UPPER PART OF THE ABDOMEN IN A CHILD (Henle).

The liver is drawn upwards in order to show its under surface and the small omentum, together with the entrance of the foramen of Winslow, into which a probe is passed.

A, quadrate lobe of liver ; S, left lobe ; D, right lobe ; Lt, ligamentum teres with its peritoneal covering forming the falciform ligament ; V, stomach ; Ct, transverse colon ; D′, duodenum ; 1, small omentum ; 2, part of great omentum ; 3, right part of small omentum, its anterior layer being divided to show its contents, viz., Ah, hepatic artery ; Vp, portal vein ; D ch, common bile duct ; Dh, hepatic duct ; and Dc, cystic duct ; 4, peritoneum reflected from the liver over the upper part of the right kidney, or hepato-renal ligament.

indicated it may be followed to the transverse fissure of the liver, where its laminæ separate, the anterior, which has already been traced from above, spreading on the adjacent part of the liver, the posterior covering the Spigelian lobe, where it will be again met with. The attachment of the combined layers continues backwards from the left end of the transverse fissure along the fissure of the ductus venosus to the diaphragm on which it runs a short way to reach the œsophagus, where the anterior lamina covers the end of that tube in front and on the left, and the posterior lamina invests it on the right and behind. From this point, as far as the pylorus, the small omentum is attached to the lesser curvature of the stomach, where its laminæ separate—one covering the anterior and the other the posterior surface of the organ—but meeting again at the great curvature, they pass down in conjunction to a variable distance before the small intestine to form the anterior part of the

Fig. 621.

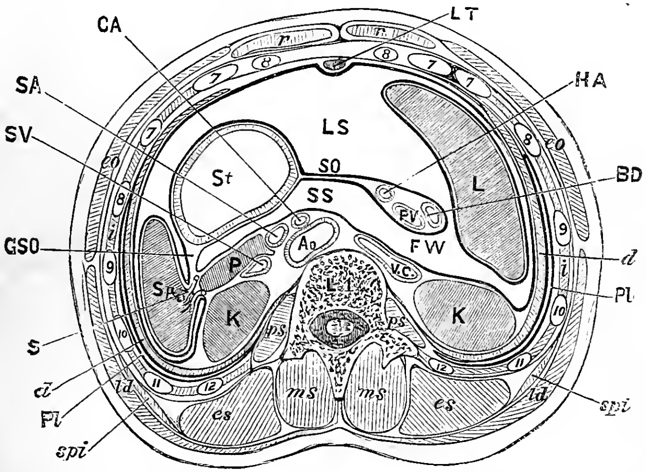

Fig. 621.—Diagram of a horizontal section through the abdomen at the level of the foramen of Winslow (R. J. Godlee).

L1, first lumbar vertebra; 12, 11, 10, &c., successive ribs; *r*, rectus muscle; *eo*, external oblique; *ld*, latissimus dorsi; *spi*, serratus posticus inferior; *i*, intercostal muscles; *es*, erector spinæ; *ms*, multifidus spinæ; *ps*, psoas; *d*, diaphragm.

Ao, aorta; V.C, inferior vena cava; C A, coronary artery; S A, splenic artery; S V, splenic vein; S, splenic vessels cut as they enter the spleen; H A, hepatic artery; P V, portal vein; B D, common bile duct.

L, liver; L T, ligamentum teres or round ligament of the liver; St, stomach; Sp, spleen; P, pancreas; K, kidney; LS, large sac of peritoneum; S S, small sac; S O, small omentum; G S O, gastro-splenic omentum; F W, foramen of Winslow; Pl, pleura.

The peritoneum is represented by a thick dark line. It can be traced from the middle line anteriorly, where it is seen investing the round ligament of the liver and forming the commencement of the falciform ligament, along the right side of the abdominal wall, over the front of the right kidney, to the inferior vena cava where it forms the posterior boundary of the foramen of Winslow; from the latter spot the small bag extends over the pancreas and left kidney nearly as far as the spleen, and then is reflected backwards along the back of the small omentum to the front of the foramen; here becoming large bag again, it turns round the hepatic vessels, forms the anterior layer of the small omentum, covers the front of the stomach, forms the gastro-splenic ligament or omentum as it is reflected on to the spleen, which it invests almost completely, and is thence continued along the diaphragm and abdominal wall back to the middle line.

great omental sac, and then turn up to form its posterior wall. Meeting next with the transverse colon, the two laminæ separate, and enclose that intestine, but meet again behind it to form the transverse meso-colon. This extends back to the lower border of the pancreas, from which its inferior layer is continued down over the posterior wall of the abdomen, and forms the mesentery, where it has been already recognized. The superior layer, on the other hand, which, as will be understood, belongs to the lesser sac, covers the front of the pancreas, the cœliac artery and its main divisions, the upper part of the left kidney, and the portion of the diaphragm between the aortic and caval orifices, and may extend to the left end of the pancreas and gastric surface of the spleen, partially investing the latter organ and forming part of the gastro-splenic omentum. It then goes forwards on the Spigelian lobe to the transverse fissure, and the line of attachment of the lesser omentum of which it then becomes the posterior layer. More to the right the layer in question passes over the vena cava, and continues into the general peritoneum beyond the foramen of Winslow. The gastric and hepatic arteries, especially the former (Huschke), may raise the membrane into folds which project into the cavity.

From the description given it will be understood that, as the sides or walls of the great omental bag consist of two peritoneal layers, its whole thickness (in its usually empty and collapsed state) will comprehend four layers. But although the bag may be inflated in its whole extent in the infantile body, its sides afterwards cohere, and it becomes impervious in its lower part. Fat, moreover, accumulates between its laminæ; long slender branches also pass down into it from the gastro-epiploic vessels.

The part of the membrane just described, which is attached to the great curvature of the stomach and transverse colon, and which is connected also with the gastro-splenic ligament (or omentum), is usually named the *great or gastro-colic omentum.* This may reach the hepatic flexure and pass a certain way down on the right colon, and this part has been distinguished by Haller and others as the *omentum colicum.* The great omentum (proper) usually reaches lower down at its left border, and it is said that omental inguinal herniæ are more common on the left side.

The description now given of the relation of the omentum to the mesocolon agrees with the appearances most frequently seen in the adult subject, and with the account usually given in English works of Anatomy; the exterior (here also posterior) layer of the great omentum being described as separating from the layer within, belonging to the omental sac, when it reaches the transverse colon so as to pass behind or below that viscus, and as proceeding thence backwards to the abdominal wall as the posterior or lower layer of the transverse meso-colon. It was, however, long ago pointed out by Haller, and the view has been confirmed by the observations of J. F. Meckel, J. Müller, Hansen, and Huschke, that in the fœtus, and occasionally in the child, or even in the adult, the two ascending layers of the omentum, though adherent to the transverse colon, may be separated from it and from the transverse meso-colon, proving that the transverse meso-colon is really a distinct duplicature of peritoneum. This view has been adopted by Holden and Luschka in their more recent works, and has been verified by Allen Thomson. Figures 619 A, and B, show diagrammatically the difference of the two views.

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EMBRYOLOGY.

ORIGIN AND DEVELOPMENT OF THE BODY AND ITS ORGANS.

In the preceding parts of this work the anatomy of the body has been described chiefly in the adult or fully-formed condition. In the following section it is proposed to bring together the principal facts which are known regarding the first origin of the human organism from the ovum, and the successive changes of development in the embryo or fœtus* by which it attains its complete form and structure. As, however, the knowledge derived from direct observation of the human ovum is still insufficient for a detailed history of its development, more especially in its earlier stages, it will be necessary to refer frequently to the corresponding phenomena as ascertained to occur in mammals and birds, and even in some other animals lower in the scale. In treating of this subject attention will be mainly given to the morphological view, the development of the textures having already been described in the histological part of this volume.

I. THE OVUM BEFORE EMBRYONIC DEVELOPMENT.

Our primary object being the description of the origin and changes of the organic elements out of which the new being is formed, we shall first take up the history of the ovarian ovum at the time when it is approaching maturity, and is about to leave the ovary, reserving the account of the origin of the ovum itself for a later part, when we shall have to treat of the special development of the reproductive organs. We shall next trace the changes of structure in the ovum which follow upon its separation from the ovary and fecundation, and which result in the formation of its more strictly germinal part, out of which, as an organised basis of formative material, the embryo is subsequently developed.

I. THE OVARIAN OVUM.

The human ovum, like that of mammals generally, is a comparatively small spherical body of about $\frac{1}{125}$th or $\frac{1}{150}$th part of an inch in diameter, and so long as it remains in the ovary, the seat of its formation, is contained in one of the Graafian follicles of that organ. As the time of maturation approaches, while the size of the ovum itself is very little increased, the follicle undergoes great enlargement, so as to attain at last a diameter of one-sixth or one-quarter of an inch or even more. This enlargement is in great part due to the increase of the albuminoid fluid which occupies a large part of the interior; but it is of course also attended with a great multi-

* It has been customary to make a distinction between the terms "embryo" and "fœtus" by applying the first to the earlier and the second to the more advanced stages in the development of the new organism; but although such a distinction may be convenient, it is not always maintained by authors, and the terms are sometimes used indifferently.

plication and extension of the cells which constitute the so-called *tunica granulosa* surrounding the interior, and of the substance of the follicular wall itself. The ovum is imbedded in a thickened portion of the *tunica granulosa*, which since the time of Von Baer has received the name of *discus proligerus*, and is thus placed near the inside of the wall of the follicle; and when this most projecting part is fully developed, most frequently at the side next the surface of the ovary. But on this point observers differ, and at an earlier period especially it appears that the position of the ovum may vary greatly, and is not unfrequently on the deeper side of the follicle.

The small and almost microscopic body which constitutes the human ovum, like that of most mammals, which it closely resembles, possesses a very definite structure, which, as already partly explained in the Histology, is that of an organised animal cell. In this view of its nature, we recognise in it an enclosing cell-membrane or cell-wall, the protoplasmic and other contents, and among these the nucleus and nucleolus; corresponding more or less with parts which have been long familiarly known in the larger ova of birds and some other animals, under the names of yolk membrane, yolk or vitellus, germinal vesicle, and germinal spot.

As in all other animal cells, the main part of the cell substance of the ovum is essentially of the nature of protoplasm, but in the yolk the simple and homogeneous protoplasm is more or less mixed or associated with a different kind of substance, viz., the vitelline granules or corpuscles, which are not immediately or directly connected with the formative processes, but yet serve in a secondary or subsidiary way for the nourishment of the protoplasm and the parts developed out of it. Hence the distinction in most if not in all ova which has been recognised since it was made by Reichert in 1840 (No. 18), between the germinal or formative yolk substance and the nutritive or food yolk. It is mainly on the wide variation in the relative quantity and disposition of these two components of the ovicell that the great differences depend which are observable among the ova of different animals.

Different Forms of Ova.—The human ovum and that of mammals belong to a group of ova in which the proportion of food-yolk is very small, while that of birds, reptiles, and elasmobranch fishes is distinguished by the very large quantity of this material, as well as by the proportionally large size of the whole ovum. In the egg of birds the yolk (which alone is to be compared to the ovarian ovum of mammals) consists in great part of large vitelline corpuscles or spheroidal groups of granules, and the primary seat of embryonic development is limited to the small whitish spot called cicatricula, about $\frac{1}{6}$ of an inch in diameter, which lies close to the pedicle in the ovarian capsule, and in a newly laid egg on the side of the yolk which naturally floats uppermost. The germinal vesicle, which is of considerable size, $\frac{1}{60}$ to $\frac{1}{50}$th of an inch in diameter, lies embedded in the centre of the cicatricula so long as the yolk remains within its ovarian capsule, and it is to this part, composed of comparatively pure protoplasm, that the first changes connected with embryonic development are restricted. Thus the centre of the cicatricula and place of the germinal vesicle have come to be recognised as the upper or germinal pole of the egg, and to be distinguished from the opposite lower side of the yolk which may be termed the antigerminal or nutritive pole. So also it has been customary to distinguish such ova as those of birds by the term *meroblastic*, as

indicating that a part only of the yolk is directly or primarily germinal or engaged in embryonic development. In the ovum of mammals, on the other hand, the whole yolk undergoes from the first the formative changes which result in the production of an embryo, and such ova have hence been named *holoblastic*. But though the distinction here mentioned is undoubtedly well founded and important, and the terms applied to the two most contrasting forms are so far appropriate, it appears that the intermediate gradations and varieties in the relative quantity and disposition of the germinal and nutritive portions of the yolk are so numerous, that it is found impossible to make a complete subdivision of the ova of animals according to this character.

But while the mature ovarian ova of birds and mammals appear at first to differ very widely from each other, a comparison of intermediate forms and the observation of their earlier condition shows in a convincing manner that they have essentially a homologous structure, and that notwithstanding the very large size and the apparent complexity of structure in the egg of the bird, both kinds of ova have in common the elementary form of the simple animal cell.

It is obvious that the great difference in size between the avian and the mammalian ovum has reference to the mode of nutrition of the embryo in the progress of its development, as modified in the one case by the complete separation of the egg from the parent body, which necessitates the provision within it of all the nourishment required for the whole duration of incubation ; and in the other case by the dependent and attached condition of the ovum and its annexes which enables them to draw a supply of nutriment from the parent during the whole of gestation.

MAMMALIAN OVUM.

The Yolk Substance.—In the mammalian or human ovarian ovum which is approaching maturity, the yolk substance forms a well-defined spherical mass, completely filling the cavity of the containing membrane. The yolk is at no place perfectly clear or homogeneous, but exhibits throughout a certain turbidity from minute granules imbedded in the purer protoplasm. The amount of yolk granules, which varies considerably in different animals, is small in the human ovum, and in general the granules are of smaller size and in less number near the

Fig. 622.

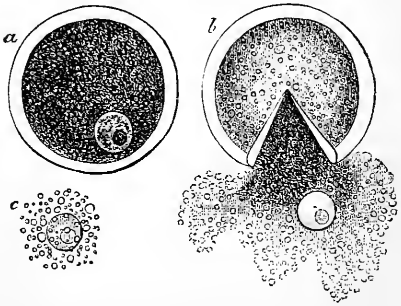


Fig. 622.—Ovarian ovum of a mammifer. $\frac{200}{1}$. (A.T.)

a, the entire ovum, viewed under pressure ; the granular cells have been removed from the outer surface, the germinal vesicle is seen in the yolk substance within ; *b*, the external coat or zona burst by increased pressure, the yolk protoplasm and the germinal vesicle having escaped from within ; *c*, germinal vesicle more freed from the yolk substance. In all of them the macula is seen.

surface of the yolk and in a space immediately surrounding the germinal vesicle. The yolk granules, or yolk corpuscles, as the larger may

be termed, are chiefly spherical in form, and are of the most various sizes, from the minutest molecules up to the diameter of $\frac{1}{1000}$ or $\frac{1}{1500}$th of an inch. They are different in composition from the clearer protoplasm, consisting mainly of protagon with fat and some other ingredients.

Fig. 623.

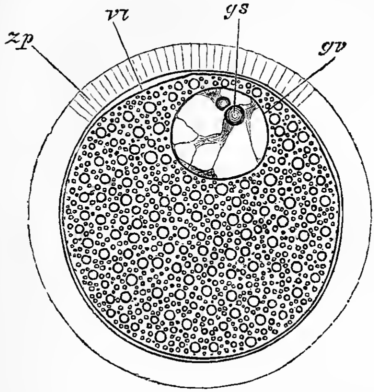


Fig. 623.—OVUM OF THE CAT; HIGHLY MAGNIFIED. SEMI-DIAGRAMMATIC. (E.A.S.)

zp, zona pellucida, showing radiated structure; *vi*, vitellus, round which a delicate membrane was seen; *gv*, germinal vesicle; *gs*, germinal spot.

They are enclosed in the substance of the more homogeneous protoplasm. The latter presents in the living state all the characters of this substance, sometimes exhibiting the finely radiated linear or fibrillar structure which belongs to its growing condition, and possessing the amœboid contractile property which is known to characterise most of its forms.

Germinal Vesicle.—While the protoplasm and vitelline granules constitute the main part of the cell-substance of the ovum, the germinal vesicle is an invariable constituent and forms its nucleus. In the ovum which has not yet arrived at complete maturity this body has a spheroidal shape, and consists of a matrix containing nucleoplasm enclosed in a fine but distinct homogeneous vesicular membrane, and is for the time situated in a clearer part of the yolk protoplasm near the surface on one side which thus becomes the germinal pole. Its size in mammals generally is about a fourth part of the diameter of the ovum, and therefore in the human ovum it may be about $\frac{1}{500}$th of an inch in diameter, being actually smaller but proportionally larger than in birds. The substance of the germinal vesicle corresponds in all respects with the usual contents of growing cell-nuclei, and may therefore be described as nucleoplasm.

Germinal Macula or Spot.—In mammals there is generally one principal nucleolus of a regular spherical or lenticular form, and presenting not unfrequently a well-defined outline. This is the macula germinativa of Rudolf Wagner, now generally recognised as corresponding to the cell-nucleolus. In mammals, however, as in other animals, the macula or nucleolus may be subdivided into several, of which one is usually larger than the rest; and in this one we may perceive an internal division into smaller opaque granules. The nucleolus appears, as in other cells, to consist mainly of a granular modification of the cellular nucleoplasm.

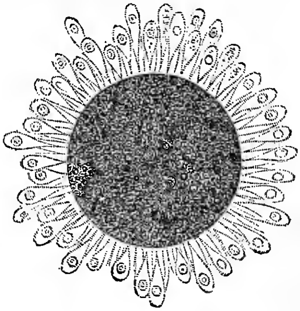
Zona Pellucida.—The most obvious enclosing membrane of the mammal's ovum is that already referred to as the zona pellucida,—a name given to it by Von Baer on account of the appearance which it presents, in a nearly ripe ovum extracted from a Graafian follicle, of a clear broad band lying between the opaque yolk substance within and the granular cells of the proligerous disc which adhere to it externally.

This vesicular envelope of the ovum is of considerable thickness and

Fig. 624.—MATURE OVARIAN OVUM OF THE GUINEA-PIG (from Bischoff.) $\frac{350}{1}$

The zona pellucida is hidden by the adherent cells of the membrana granulosa, which have assumed a pediculated form next its surface. The finely granular yolk substance fills the cavity of the zona. The germinal vesicle has disappeared.

Fig. 624.



of great strength, bursting only under strong pressure or by the aid of cutting instruments. Under a moderate magnifying power, when freed from the adherent cells of the proligerous disc, it appears homogeneous; but when subjected to higher magnifyers, such as 500 or 600 diameters, it frequently exhibits a linear radiation through its thickness, which bears some resemblance to the more distinct radiated and porous structure in the egg covering of osseous fishes, insects, and some other animals. And some are of opinion that the pores of the covering of the mammal's ovum are capable of transmitting minute granules or even cells from the exterior into its cavity; but it seems probable that such a condition of the pores is not constant, and that their occasional enlargement, as observed by Lindgren (No. 65) and Von Sehlen may depend upon unnatural circumstances (No. 66).

In 1841 Reichert described a second more delicate membrane as immediately surrounding the yolk substance in the mammal's ovum, and more recently Edw. Van Beneden (No. 57) has affirmed the existence of such a membrane, and adheres to this opinion in the account of his latest researches (No. 63). This membrane he finds to be formed in the mammal's ovum as it approaches maturity, and to remain visible for some time after it has left the ovary. F. M. Balfour (Nos. 32 and 62) is inclined to adopt the same view, while other embryologists still entertain doubts as to its existence.

In 1840 Barry thought he had discovered in the rabbit's ovum a distinct foramen or perforation of the zona pellucida similar to the *micropyle* of fishes, insects, and some other animals, and Pflüger and E. V. Beneden for a time supported this view. But the last observer has from his most recent observations been led to abandon it, and as many other embryologists have sought in vain for this aperture, it may now with certainty be considered as absent from the mammiferous ovum in the more distinct form described by Barry, although occasionally, as before stated, minute pores or radiating canals are seen to pierce the zonal membrane.

The Mammalian ovum was discovered by Von Baer in 1827 (No. 49). The germinal vesicle, which had been made known in Birds by Purkinje in 1825 (No. 48), was first described in the Mammal's ovum by Coste in 1833 (No. 50, i.), having also been independently observed by Thomas W. Jones in 1834 (No. 51, i.). The macula or nucleolus was first pointed out by Rudolph Wagner in 1835 (No. 52, i. & ii.). See the Bibliography, Nos. 47 to 66.

II. MATURATION OF THE OVUM AND SEPARATION FROM THE OVARY.

It was long known that at or near the time of the full maturation of the ovum and its leaving the ovary, both in birds and mammals, the germinal vesicle, which had gradually approached the surface of the ovarian ovum in the later stages of its development, finally disappeared or was lost to view. It was not certain however that this occurred in all

animals, nor was it known how the disappearance was to be explained, and whether any part or how much of the substance of the germinal vesicle, as was vaguely conjectured, might have remained to undergo further changes, to combine with the yolk, or to form the basis of an

Fig. 625.

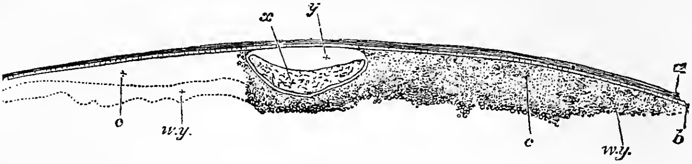


Fig. 625.—Vertical section through the germinal disc of the ripe ovarian ovum of the fowl, in its capsule. (From Balfour.)

a, Connective tissue of the ovarian capsule ; *b*, its epithelium, close to which is the vitelline membrane of the ovum ; *c*, granular protoplasm which undergoes segmentation ; *w.y*, white yolk substance ; *x*, substance of the germinal vesicle shrivelled up ; *y*, space left by this shrinking within the membrane of the vesicle.

embryonic nucleus. Improved modern methods of histological research have led to the discovery of some of the phenomena of retrogression of the germinal vesicle and the foundation of the germ of a very remarkable kind, of which a short account will be given at this place.

Exclusion of the Polar Globules, and Formation of the Female Pronucleus.—These phenomena of retrogression in the germinal

Fig. 626.

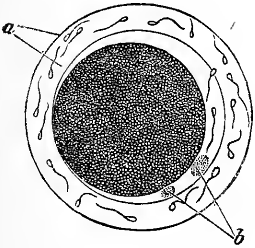


Fig. 626.—Ovum of the rabbit from the fallopian tube, twelve hours after impregnation. (From Bischoff.)

In the zona *a*, spermatozoa are seen ; *b*, two hyaline globules or polar bodies within the cavity left by the shrinking of the yolk.

vesicle are intimately connected with another appearance which since its first discovery by Dumortier in 1837, and further investigation by F. Müller in 1848, has been familiar to embryologists in a very wide range of animals, viz., the formation or extrusion from the yolk at the time of complete maturation of the so-called *polar* or *directing* globules, of which the relation to the germinal vesicle has only recently received a more minute investigation, although various more or less probable suppositions had been from time to time formed as to their nature.

The most precise and satisfactory of the recent observations now referred to have been made chiefly upon the ova of animals comparatively low in the scale, but we are not without evidence that nearly similar phenomena occur also in the higher animals and especially in mammals. We shall first describe shortly the results of observations made by Bütschli, Fol, and Hertwig on the ova of some Echinoderms and Heteropods ; referring the reader to the works quoted at p. 22 of this volume, and to the very clear account of the phenomena given by Balfour (No. 32, vol. i. p. 55, and No. 76).

In the Asterias glacialis, according to Fol, as soon as the ripe ovum is

detached from the ovary and placed in sea water, the germinal vesicle, which was previously of a regular spherical shape and presented the nuclear reticulum and all the usual characteristics of such structures, loses its external membrane and its internal reticulum, takes an irregular outline and undefined structure, and becomes to some extent confounded with the vitellus. The germinal macula also gradually disappears. Between the remains of the germinal vesicle and the surface of the yolk there now appears a nuclear spindle or double cone terminating externally in a star-like arrangement of the protoplasm. Soon afterwards another star appears and the nuclear spindle lies horizontally between

Fig. 627.

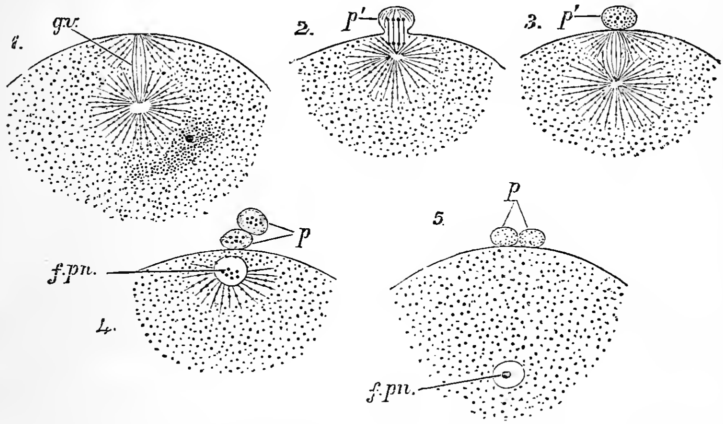


Fig. 627.—Stages in the formation of the polar globules in the ovum of a star-fish (from Hertwig.)

gv, germinal vesicle transformed into a spindle-shaped system of fibres ; *p'*, the first polar globule becoming extruded from the surface of the ovum ; *p*, polar globules completely extruded ; *f.pn*, female pronucleus.

the two stars. Oscar Hertwig observed phenomena very nearly similar in another Echinoderm (Asteracanthion), but it was not determined by either of these sets of observations, what share, and whether any, the macula took in the changes which occurred ; but further observations by Fol on one of the Heteropodes (Pterotrachæa) made it certain that the metamorphosis of the germinal vesicle results in the formation of a nuclear spindle with the two stars lying near the surface of the ovum, and that these phenomena, as was well known also in other animals, are quite independent of fecundation.

The next change consists in the spindle assuming a vertical instead of a horizontal position, and in the subsequent projection of one end or star in a protoplasmic prominence or knob from the surface of the yolk. By a constriction which follows in the outer part of this prominence, a small spherical mass of clear protoplasm constituting the *first polar body or globule* is separated and takes its place close to the original site of the germinal vesicle in a space now formed by the shrinking of the yolk between the surface of that body and the enclosing membrane.

The process of nuclear division being repeated in the spindle-shaped body, another polar globule is separated in a manner similar to the first;

and the irregular remains of the germinal vesicle within the yolk gradually assume the more regular spherical form and clear appearance of a nucleus, which sinking more deeply into the yolk now constitutes the *female pronucleus*.

It is probable that similar phenomena occur in all animals. They have been observed more or less completely in Petromyzon, the Sturgeon, Osseous Fishes (Trout), Amphibia, and among Mammals in the Rabbit and Bat. The following are the principal results of the observations of Edw. Van Beneden on the latter two animals.

The germinal vesicle of the ovum which approaches maturation flattens out, and rising to the surface fuses with the superficial part of the yolk protoplasm in a lenticular form. The germinal spot proceeding to the surface of this becomes discoid, while the membrane of the germinal vesicle vanishes or unites with the disc. The plasma of the nucleus collects into a nucleoplasmic mass, and along with the nuclear disc remains for a short time within the ovum. Soon afterwards, however, a polar body is found outside the yolk, composed of two parts, of which one stains deeply in the same manner as the discoid part of the nucleus, while the other resembles the nucleoplasmic substance in not staining. Van Beneden looks upon these parts of the polar body as the ejected products of the germinal vesicle ; but Balfour considers it more probable that a part of the germinal vesicle remains in the ovum to form the female pronucleus.

The shrinking of the yolk coincides with the expulsion of the first polar body which usually takes place before the rupture of the follicle ; the second polar globule is more frequently expelled after the ovum has entered the tube, and along with its appearance there is a further shrinking of the yolk ; but all these phenomena are quite independent of fecundation or any influence of the male sperm.

Separation from the Ovary.—It is now well ascertained that the maturation and the discharge of the ovarian ova and the accompanying changes to which the Graafian follicles are subject recur periodically during the breeding period,—in the human female at every successive menstrual term, and in animals at the times of heat,—and that these changes take place independently of the influence of the male or of impregnation (Bischoff, No. 67).

In animals, such as the sheep or dog, when the state of heat has lasted some days, and in the human female at or near the time of the menstrual flow, the ovum is discharged by the rupture of the thinner and most projecting part of the Graafian follicle. The aperture takes place at a spot, the macula or stigma, which is non-vascular, is small and with irregular or ragged edges, and its formation by a solution of continuity of the tissue is preceded by increased vascularity in the neighbourhood. The ovum in escaping remains imbedded in the cells of the discus proligerus which adhere closely to it, and it is probably accompanied by parts of the tunica granulosa and some of the fluid of the follicle. These are pressed out of the follicle in part by the elastic reaction of the dilated theca, and in part by the increasing development of new cellular elements in the interior of the follicle.

By a mechanism which it does not belong to our present view to describe, the ovum with its accompaniments is received into the wide fimbriated mouth of the Fallopian tube, and descending in that canal, if not fecundated, gradually disappears or is lost; but if subjected to the fertilizing influence of the semen, begins to undergo the changes of development which lead to the formation of an embryo.

The Graafian follicle, as already indicated, comes soon to be occupied by the

body named from its yellow colour *corpus luteum*, and it is important to observe that this takes place in all cases of the rupture of a follicle, whether or not it has been followed by impregnation. The changes involved in the formation of this body and its structure have been already described at p. 336 of this volume.

III. FECUNDATION OF THE OVUM.

The process of fecundation, which will be considered here only in its relation to the formation of the germ, consists, in its most general acceptation, essentially in the union of the male and female generative elements. For the history of the male generative element we refer the reader to the account given at p. 698 of this volume.

Introduction of the Spermatozoa into the Ovum.—The fact of the actual entrance of spermatozoa within the zona or covering of the mammiferous ovum was first observed by Martin Barry in 1843, and although his statement was received with considerable hesitation by his contemporaries, it has since been repeatedly confirmed by the minute and careful investigation of many observers.

In certain animals the spermatozoa have been seen to enter the cavity of the ovum by an obvious micropyle aperture, as first observed by Ransom in fishes (No. 72), and by Meissner and Leuckart in insects; but in mammals and other animals in which no such aperture exists, it is not yet clearly understood in what manner the spermatozoa make their way through the consistent membrane of the ovum.

Changes in the Ovum and Spermatozoa giving rise to a Male Pronucleus.—In mammalia, although the spermatozoa are ascertained to pass in numbers through the zona, they have not been

Fig. 628.

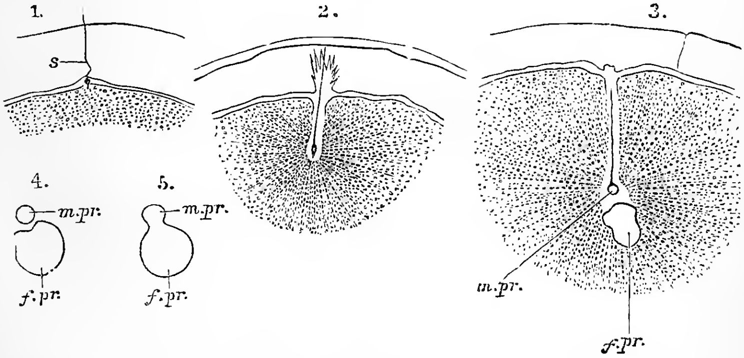


Fig. 628.—Fertilization of the ovum of an echinoderm (Selenka.)

s, spermatozoon; *m.pr*, male pronucleus; *f.pr*, female pronucleus.

1. Accession of a spermatozoon to the periphery of the vitellus; 2. Its penetration, and the radial disposition of the vitelline granules; 3. Transformation of the head of the spermatozoon into the male pronucleus; 4, 5. Blending of the male and female pronuclei

observed in any case to penetrate or combine with the substance of the yolk. It is extremely probable that such combination does take place, but we only know of this occurrence by observations made on the lower animals, which, however, throw so much light on the whole process of fecundation that it is proper to give an account of them in this place.

In this account we shall follow mainly as before the statements of Fol and Hertwig, together with some others as described in Balfour's very clear account of this subject.

In the Asterias glacialis, the female pronucleus, formed simultaneously with the ejection of the polar globules and independently of fecundation, having retired towards the centre of the ovum, a number of spermatozoa penetrate with active motions the mucilaginous egg covering, with their heads directed inwards and their tail filaments extending radially outwards.

In Selenka's account of these phenomena as illustrated by the accompanying figures a clear canal-like space remains in the track of the spermatozoon.

One of the spermatozoa more advanced than the rest comes now to be surrounded and ultimately combined with a prominent part of the yolk substance, and, the tail remaining motionless and subsequently disappearing, the head, or it may be some other part of the spermatozoon, is now gathered together into the form of a nucleus, and, sinking to some depth into the substance of the yolk, becomes surrounded with the radiated lines known to belong to such structures. It is now, in fact, converted into the *male pronucleus*.

Fusion of the Male and Female Pronuclei, and Production of the First Segmentation Sphere.—The male pronucleus gradually approaches the site of the female pronucleus; and as soon as it comes in contact with it, the latter, which was previously motionless, assumes a new activity, and the two pronuclei, impelled perhaps by the amoeboid movements of the yolk protoplasm which accompany the change, finally unite or are fused into one.

The result of this union is the formation of the first *embryonic* or *segmentation sphere*, or *Blastosphere*, which may be regarded as a nucleated protoplasmic cell, containing the products of the male and female generative nuclei, or some portion of them, combined with the yolk protoplasm of the ovum.

In mammalia Van Beneden has shown that the first segmentation nucleus owes its origin to the fusion of two previously existing nuclei which could be no others than the male and female pronuclei. In Petromyzon, Calberla, Kupffer and Benecke have demonstrated that a single spermatozoon at first enters the ovum, and the researches of Bambeke and Hertwig make it extremely probable that in Amphibia similar phenomena attend the maturation and fecundation of the ovum, while Oscar Hertwig has traced in Echinus lividus the entrance of the spermatozoon into the ovum and its transformation into the male pronucleus. Precisely similar phenomena have been ascertained by Salensky to occur in the sturgeon; so that there is good reason to believe them to be universal among bisexual animals. (See Balfour, No. 32 and No. 76.)

Differences in the details of these phenomena may occur in different animals, more especially according as impregnation may take place before or after the separation of the polar globules. In the former case, as in Echinus, the male pronucleus is comparatively small, but in the latter case, as in Hirudinea, Mollusca, and Nematodes, in which the polar globules are not fully separated till after impregnation has taken place, the male pronucleus becomes as large as the female.

It appears further that while one spermatozoon is probably sufficient for fecundation in most instances, a greater number may occasionally penetrate the yolk substance, and Fol states that when this occurs each spermatozoon has a distinct pronucleus formed round it, and that several of these may combine with the female pronucleus.

Ever since the similar origin of the generative elements of the two sexes has been ascertained, it has been customary to regard fecundation as consisting essentially in the union of the male and female generative cells: but we can now attach a much more definite idea to this view when we know that the act of fecundation consists in the fusion of a male and female pronucleus, of which one has sprung from the remains of a primitive ovicell, and the other is the product of a primitive sperm cell, and that both of these have had their origin in similar elementary structures of the parent while in the embryo stage of its existence. (Balfour, No. 32. Balbiani, No. 64, and Bibliogr. Nos. 67 to 76.)

IV SEGMENTATION OF THE FECUNDATED OVUM, AND FORMATION OF THE BLASTODERM.

It is a general fact among bisexual animals that within a very short time after the fertilization of the ovum has been effected by the combination of the sexual elements, the blastosphere or nucleated mass of productive protoplasm which results from the act of union proceeds to undergo a process of division and multiplication after the manner of cell cleavage, and by the ordinal repetition of that process for a considerable number of times there is eventually produced a collection of *blastomeres* or nucleated cells, out of which the further development of the embryo subsequently takes place. To this mass of cells capable of embryonic development the name of protembryo or primitive embryo might be applied, but it is the same which has been called *germinal membrane* or *blastoderm* in the higher animals, because of the flattened or laminar form which the collection of its cells generally presents.

To this process of cell division and multiplication in the fecundated ovum the names of yolk cleavage, or more strictly germ-segmentation are applied. Though common to all the metazoa it presents many and great variations in the different classes of animals, and even among some allied families. Here we must confine our attention mainly to those forms in which the phenomena tend to illustrate the process as it occurs in Mammalia.

Different Forms of Segmentation among Animals.—The more important of these varieties are obviously related to the difference in the proportion of the nutritive and germinal material in the holoblastic, meroblastic, and intermediate forms of ova. In the case of mammals, the whole mass of the yolk is subject to this change, or is immediately involved in the process of cell division, while in the meroblastic ovum of the bird the first cleavage and consequent formation of a blastoderm is limited to that small portion of the yolk which is termed the germinal disc or cicatricula, and which is alone the seat of the earliest phenomena of development.

This difference constitutes the distinction between *total* and *partial* segmentation, of which we shall have to consider more fully the phenomena, and with regard to which it is only necessary to say further at this place that there is a close inverse relation between the extent of the segmenting process and the quantity of the nutritive yolk substance which is associated with the purer protoplasm of the ovum; and thus through the amphibia and other animals, besides variations of other kinds, all possible gradations are to be found in the proportion of the substance of the ovum which is primarily involved in the cell-forming process resulting from segmentation.

The intermediate form of segmentation which occurs in the Amphibia, as in the frog or newt, is so instructive that it will be proper to introduc

a short description of it at this place before proceeding with that of mammals and birds.

Complete and Unequal Segmentation in Amphibia.—In the batrachian ovum the segmentation may be regarded as total or complete in so far that it extends from the first throughout the whole mass of the yolk, but it may be considered as *unequal* in this respect, that there is in some sort a concentration of the process towards the germinal pole, where the cells resulting from the yolk cleavage are smaller and more numerous, while they become gradually larger and less distinctly separated towards the opposite or nutritive pole—a difference which is manifestly related to the purer condition of the egg protoplasm in the neighbourhood of the first, which was the original seat of the germinal vesicle, and the larger quantity of nutritive yolk accumulated at the lower or anti-germinal pole. The accompanying diagram copied from Ecker gives a sufficiently clear view of the successive steps of the process; 1 representing the undivided condition, 2 the first vertical cleft which divides the whole yolk into two, 4 indicates the stage at which by a second vertical cleft the yolk is now divided into four segments. In these two first stages the vertical clefts proceed downwards from the upper or germinal pole, where they cross each other at right

Fig. 629.

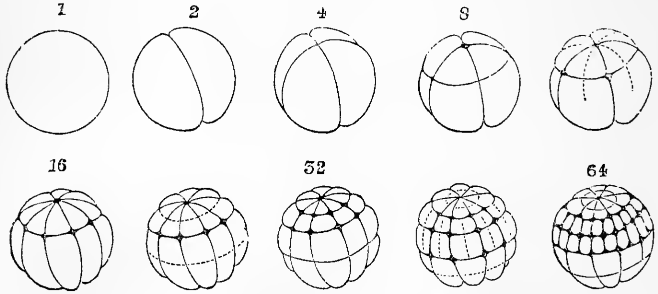


Fig. 629.—UNEQUAL SEGMENTATION IN THE EGG OF THE FROG (from Balfour after Ecker.)

Ten stages are represented; the numbers over certain figures indicate the number of segments at each of these stages; in the intervening figures the fissures are in progress of formation.

angles, to the lower or nutritive pole. In the next stage, however, marked 8, in which that number of segments have appeared, the new cleft is horizontal and parallel to the equator of the sphere, but at some distance above it. This again is succeeded by radial or meridional clefts which, proceeding gradually from the germinal pole, divide first the upper and later the lower segments, so as to produce first twelve and later sixteen segments, as seen in the outline numbered 16. Two equatorial clefts follow, which have the effect of dividing both the upper and lower meridional segments, so as to produce first 24 and subsequently 32 segments; and by a succession of similar alternating vertical and horizontal clefts a greater and greater multiplication takes place, but in such a manner as to give rise to more numerous and smaller and closer cells in the upper germinal and deeply coloured part and fewer and larger and looser cells below.

Up to a certain point the progression is regular, but when the number of segments has become considerable the regularity is no longer perceptible. A cavity at the same time appears, the *segmentation cavity*, which lies between the smaller cells of the upper and the larger cells of the lower division; and these two sets of cells respectively correspond to the upper and lower layers of the blastoderm of higher animals. In the Amphibia then the segmentation, though complete, is from the first unequal. (See No. 26, Tab. 23, Explanation.)

Complete and Equal Segmentation of Amphioxus and Petromyzon.—Segmentation which is at once complete and equal occurs in many of the inverte-

brate animals, but among the vertebrates or animals allied to them the only examples are those of Amphioxus and Petromyzon. In the case of Amphioxus after the successive reduplication of the yolk-spheres has proceeded to such an extent as to divide the whole into smaller uniform nucleated cells, these cells are found to have arranged themselves as a layer on the surface, while the interior is occupied by fluid, constituting thus a cellular vesicle with a segmentation cavity within ; and the first change which succeeds to this stage consists in the doubling in or invagination of one side of the cellular wall so as to give rise to a secondary cavity communicating with the exterior, while the two sides approach one another so as gradually to narrow and at last obliterate the original cavity which lay between them. The part which remains outside forms the external layer or ectoderm, and that which is doubled in is the internal layer or entoderm. The protembryo or blastoderm thus assumes the form of the bilaminar *gastrula* of Haeckel, communicating with the exterior by the now narrowed aperture called blastopore, and representing in fact the simplest form of an alimentary cavity.

Complete Segmentation in Mammals.—The Mammals come next to the Amphioxus in the completeness and regularity of the segmentation, but they differ from it both in the early distinction of the upper and lower blastodermic cells and in the absence of any obvious invagination of the vesicular blastoderm.

The segmentation of the mammiferous ovum had been seen by Martin Barry, but its general features were first clearly demonstrated by the important researches of Bischoff. In more recent times much light has

Fig. 630.

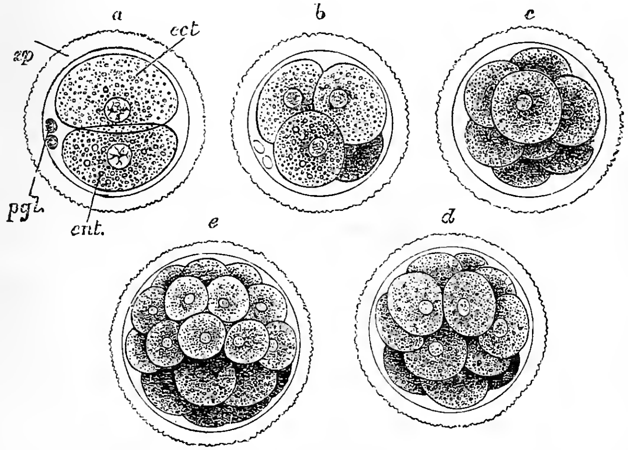


Fig. 630.—First stages of segmentation of a mammalian ovum : semi-diagrammatic. (Drawn by A. T. after Edwd. v. Beneden's description.)

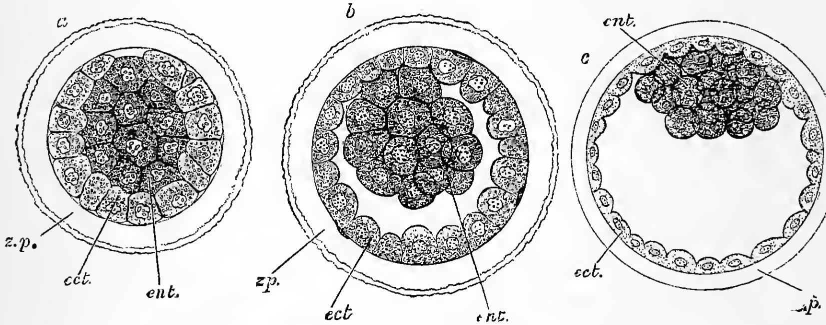
z.p, zona pellucida ; *p.gl*, polar globules ; *ect*, ectomere ; *ent*, entomere ; *a*, division into two blastomeres ; *b*, stage of four blastomeres ; *c*, eight blastomeres, the ectomeres partially enclosing the entomeres ; *d.e*, succeeding stages of segmentation showing the more rapid division of the ectomeres and the enclosure of the entomeres by them.

been thrown upon the nature of this process by the interesting researches of Edwd. Van Beneden (No. 74) and others. From the observations of Van Beneden it appears that in the ovum of the rabbit within one or two hours after the union of the male and female pronuclei the process of division of the nucleus and the primary segment sphere commences.

This, as well as all the subsequent divisions which occur, is accompanied by the usual phenomena of spindle modification of the nucleus and radial striation of the surrounding yolk protoplasm. The whole process of segmentation is accomplished in the rabbit within from 70 to 75 hours after fecundation, by which time the ova have passed through the Fallopian tubes and are entering the cavity of the uterus.

The principal phenomena as described by Van Beneden are as follows. First a complete division of the whole yolk into two spheroidal or ovoid masses takes place, the cleft seeming to depart from the place previously occupied by the polar or directing bodies. Each of these spheroids is next divided in a similar manner with the first into two, so that four result, and in a third stage the division of the four spheres brings the

Fig. 631.



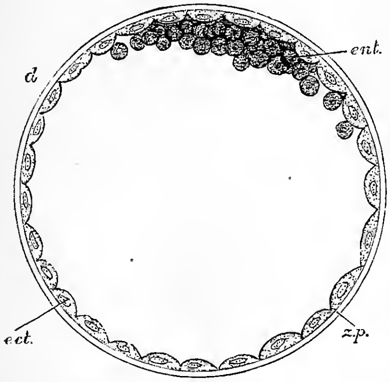


Fig. 631.—Sections of the ovum of the rabbit during the later stages of segmentation, showing the formation of the blastodermic vesicle (E. v. Beneden).

a, Section showing the enclosure of entomeres by ectomeres except at one spot—the blastopore; *b*, more advanced stage in which fluid is beginning to accumulate between the entomeres and ectomeres, the former completely enclosed; *c*, the fluid has much increased, so that a large space separates entomeres from ectomeres except at one part; *d*, blastodermic vesicle, its wall formed of a layer of ectodermic cells, with a patch of entomeres adhering to it at one part; *z.p.*, *ect.*, *ent.*, as before.

number up to eight. It is to be remarked however that the size of the two spheres resulting from the first cleavage is not equal, but the one which we shall call the upper is the largest, and it is also somewhat differently affected by reagents from the lower one; and Van Beneden has suggested the view that this difference is already an indication of a distinction between the cells of the upper and lower layers of the blastoderm (Nos. 74 and 75).

When the division has reached the third stage and eight spheres are formed, these are found to have arranged themselves in such a manner that the four lower cells become more closely gathered together by one

of them taking a central position with reference to the rest, and the four upper cells at the same time show a tendency to surround and enclose the lower, which at a later period their successors do more completely.

A difference in the rate of division of the upper and lower group of spheres now becomes apparent, that of the upper being somewhat in advance of the lower; and thus in the fourth stage, while the cells of the lower group remain only four in number, the upper have divided and amount to eight. The division of the lower group then brings their number to eight and the whole yolk consists of sixteen spheres.

There is now found also to be a change in the relative size of the upper and lower groups of spheres, the latter having now become the larger and fewer, and also the more opaque and granular in their aspect.

The upper spheres at the same time show more and more tendency to spread over the surface of the lower group which are gathered together in a ball, and thus to surround and enclose them. This enclosure, however, is not complete till the tenth stage, when the whole number of spheres, or cells as they may now be called, is 96, of which 64 are those of the surface, and 32 occupy the interior.

There is a time however during which the external layer of cells, though covering the mass of inner ones, does not completely close them in, but leaves one or more of them visible by an aperture which has been compared by Van Beneden, but according to some on insufficient grounds, to the blastopore or aperture of invagination in the lower animals. This aperture is soon effaced by the union of the external cells over it, and in this stage, which may be regarded as the completion of the segmentation, the ovum is covered externally by an entire layer of nucleated and somewhat prismatic cells, while the interior is occupied by a solid mass of cells of a different character. Thus the whole segmented ovum, which is still only slightly increased in size, is converted into a hollow cellular sphere to which at a later period the name of *blastodermic vesicle* is given.

Partial Segmentation.—The process of segmentation as it occurs in mesoblastic ova contrasts widely in its more apparent phenomena with that previously described, and yet, considered as one of protoplasmic cell-division, and

Fig. 632.

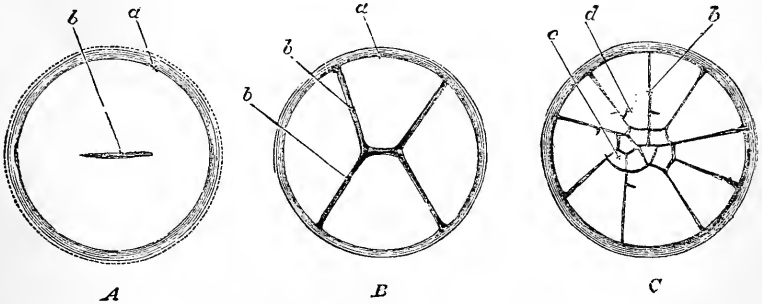


Fig. 632.—Surface views of three early stages of segmentation in the fowl's egg. (From Balfour after Coste).

A, stage of the Primary furrow; B, first Radial furrows; C, other Radial furrows with the first circular; *a*, edge of the germinal disc; *b*, primary and vertical furrows; *c*, smaller central, and *d*, larger peripheral segments.

viewed in the light of the relations of its germinal and nutritive yolk substance to each other in the ovum, the phenomena may be regarded as fundamentally similar. In the egg of the bird, as in the common fowl, the primary segmentation of the germ is limited to the cicatricula or germinal disc, and this process is accomplished during the descent of the yolk or ovarian ovum through the oviduct, and particularly in its lower part, while at the same time the egg is

Fig. 633.

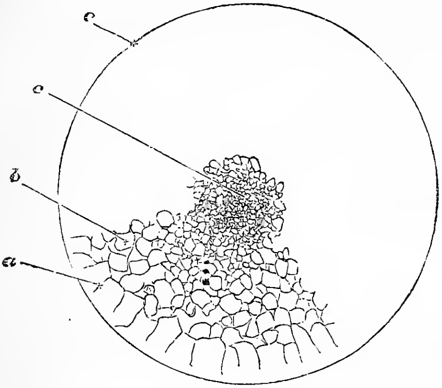


Fig. 633.—Surface view of the germinal disc of the fowl's egg in a later stage of segmentation (from Balfour.)

c, small central segmentation spheres; *b*, larger segments outside these; *a*, large, imperfectly circumscribed, marginal segments; *e*, margin of the germinal disc.

being enclosed in its accessory constituents of albumen, membrane, and shell derived from secretion previous to its being laid. This descent usually occupies in the common fowl from 16 to 24 hours or not much longer period, and the process of segmentation is therefore a comparatively rapid one.

The more obvious phenomena attending this process, as observed by Coste (No. 22, iii.) and Kölliker (No. 28 i. p. 70), consist in the occurrence, first of a groove or cleft across the cicatricula in a determinate direction, which appears to be at right angles to the long axis of the whole egg. This is soon followed by another groove, which crosses the first nearly at right angles or intersects it at opposite sides in two separate places. In a third stage the four segments of the germinal

Fig. 634.

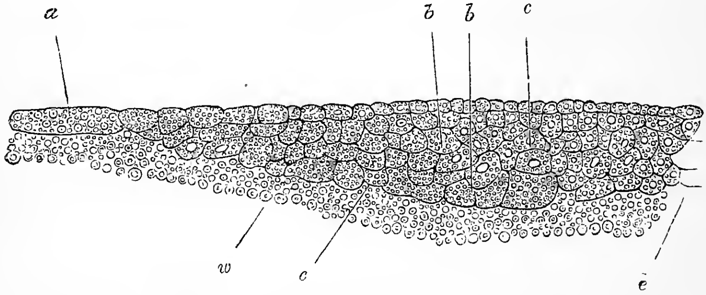


Fig. 634.—Vertical section through more than a half of the germinal disc of a fowl in the later stages of segmentation (from Balfour.)

c, indicates the middle of the germinal disc; *a*, one of the larger peripheral segments; *b*, larger cells in the deeper part of the blastoderm; *c*, edge of the blastoderm adjoining the white yolk (*w*); most of the cells contain nuclei.

disc which were separated by the two first grooves, are again divided by new grooves, each of which, like the first, has a radial disposition, so that eight segments now result. But in a fourth stage the segmenting groove takes a circular or concentric direction, and is such as to cut off a small portion at the upper angle of each of the eight radial segments close to the centre. Sixteen

segments are thus formed, and subsequently, by a less regular alternating succession of radial and concentric division the whole disc comes to be divided into smaller portions, within each of which, as appears in the end, a nucleus is formed, and which therefore have the value of true protoplasmic cells. They are in fact the precursors of the formative cells of the blastoderm. It appears further that the cells which thus result from the segmenting process are arranged in two layers, an upper consisting mainly of one range of cells which are clearer and with more defined outlines, and a lower set of cells, which are somewhat larger, more opaque and granular in their aspect and more loosely and irregularly disposed. These layers are separated from the yolk below by a cavity which may be called the segmentation cavity, and they correspond with the primitive layers of the blastoderm.

The nature of the meroblastic form of segmentation now described was first clearly understood from the observations of Kölliker on Cephalopoda in 1844; and the phenomena have since been investigated in reptiles, cartilaginous fishes, and other animals.

In the Teleostei or osseous fishes the segmentation is also partial, but with a nearer approach to the unequal cleavage of the Amphibia.

II. DEVELOPMENT OF THE OVUM IN GENERAL.

I. THE BLASTODERM.

From the preceding account of the segmentation of the ovum it appears that in the amniotic vertebrates the general result of that process is the formation of a flattened or membranous plate or layer of organised cells; and the further observation of the progress of development of the ovum shows that the whole of the genetic changes to which the parts of the future embryo owe their origin take place within, or in close connection with the cellular elements of this plate or membrane. It is essentially therefore the germinal part of the egg, and in the discoid form which it presents in birds was appropriately named by Pander *germinal membrane* (Keimhaut) or Blastoderma, and this name is equally applied to the vesicular form which it presents in mammals and some other animals.

In the sauropsida, and to some extent also in the mammalia, the blastoderm, on the completion of the primary segmentation, does not consist of one layer of cells only, but shows a tendency to division into two layers or two sets of cells, of which the external are generally the more advanced in their state of development. From their relative position these layers may be distinguished as the upper and lower, or outer and inner, primary layers of the blastoderm. Between these two layers, as they become more differentiated, at a subsequent but still very early stage of blastodermic development a third or middle layer makes its appearance, producing thus a trilaminar structure. As the result of all modern embryological research has shown that the first origin and formation of the several systems, organs, and textures of the embryo stand in definite relations to the several layers before mentioned or their derivatives, it will be apparent that the history of embryonic development, more especially in its earlier stages, is in a great measure the narrative of the organogenetic changes occurring in the upper, middle, and lower layers or cellular strata of the blastoderm.

1. **Preliminary Notice of some of the Fundamental Phenomena of Development.**—Before proceeding to consider the somewhat intricate and still imperfectly understood subject of the nature and origin of the blastodermic layers, and their relation to the phenomena of development, it may assist in some degree the comprehension of what is to

follow if we state here as briefly as possible the nature of the earliest steps in the development of the ovum and first appearance of the rudiments of the embryo. In this statement reference will be made chiefly to the phenomena as they occur in the bird's egg, while at the same time it may be mentioned that they are essentially the same in the other Amniota.

Under the influence of the heat of incubation in the fowl's egg, the germinal disc expands at its periphery and as a whole; the outer part, becoming thicker by the accumulation of formative elements derived from the yolk, constitutes the opaque area, and the central part, remaining much thinner, forms the transparent area. The upper layer of the blastoderm extends over the whole of this disc; the lower layer in its primary condition reaches only as far as the inner margin of the opaque area, becoming there continuous with the formative substance of the yolk in the thickened part which is named the *germinal wall*. After a few hours of incubation the transparent area, from being at first nearly circular, becomes oval and then pyriform;

Fig. 635.

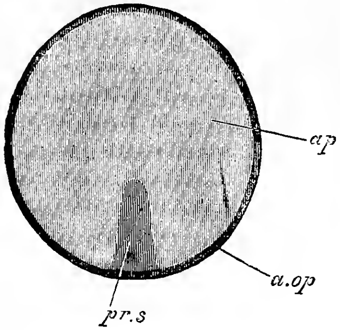


Fig. 636.

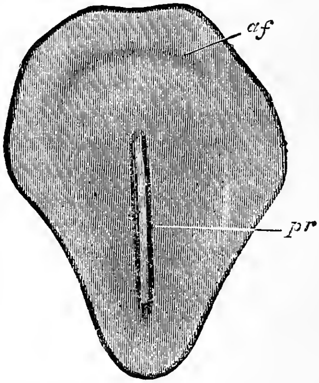


Fig. 635.—Transparent area of the blastoderm of a chick at a very early period, showing the commencement of the primitive streak. (From Balfour.)

pr.s, primitive streak; *a.p*, area pellucida; *a.op*, area opaca.

Fig. 636.—Pyriform transparent area of the chick's blastoderm with the primitive groove. (From Balfour.)

pr, primitive streak and groove; *af*, amniotic fold commencing; the darker shading round the primitive streak indicates the extension of mesoblast.

and on that side of the oval which afterwards becomes the narrow end of the pyriform space, and therefore near the margin, a sickle-shaped opacity appears (Kupffer, No. 113), which is gradually prolonged into the middle of the area and even beyond it, and as the marginal widening contracts, the whole takes the appearance of a strap-like thickening of nearly uniform diameter throughout. This is the *primitive streak* or trace, which is the first indication of the lineaments of the future embryo. A groove very soon appears in the upper surface of the streak, the *primitive groove*, in which we shall afterwards have to notice certain depressions or perforations of the blastoderm which are of great embryological interest. About the sixteenth hour there is formed in the wider forepart of the transparent area a considerable thickening of the upper layer, which is soon divided by a median

groove into two ridges, extending backwards so as to enclose partially the front of the primitive streak; they unite or run into one at the forepart. These ridges and the thickened plates within them are the *dorsal ridges* and *medullary plates* which form the commencement of the brain and spinal marrow or cerebro-spinal axis of the embryo. It will afterwards be shown that the primitive streak and groove are comparatively evanescent and unimportant structures as regards the organs of the future embryo.

The dorsal ridges and medullary plates, continuing to grow steadily, extend themselves from before backwards, so as to encroach more and

Fig. 637.

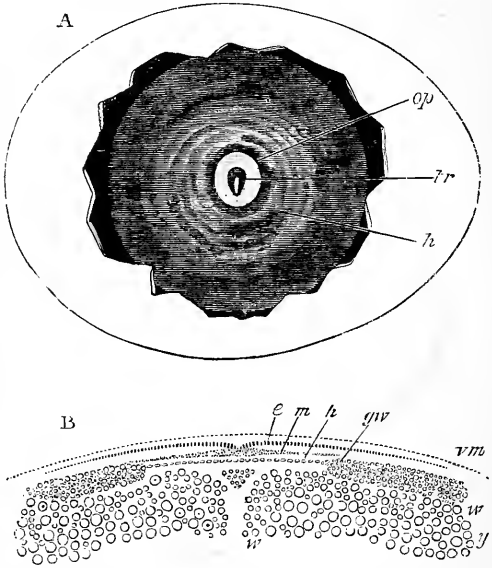


Fig. 637. — Surface view and diagrammatic section showing the relation of the primitive streak and blastoderm to the yolk in a fowl's egg after twelve hours of Incubation. (A. T.)

A, surface view, natural size; *op*, opaque area; *tr*, transparent area, pyriform, and showing the primitive streak in its narrower portion; *h*, haloes of the yolk surrounding the germinal disc; B, section across the disc, and a part of the yolk in the region of the primitive streak, magnified about ten diameters; *vm*, vitelline membrane indicated by a dotted line; *e*, the epiblast in the region of the primitive streak, showing the depression in the middle of the upper surface formed by the primitive groove; *m*, the mesoblast beginning to be formed, and spreading outwards from the epiblast at the primitive streak; *h*, the hypoblast, extending across below and passing at the sides into the germinal wall of the yolk, *gw*; *w*, the white; and *y*, the yellow or granular yolk substance.

more upon the primitive streak, which they, along with the mesoblastic columns on either side of them, partly extrude and partly enclose; and the ridges, rising and approaching one another, unite together along the dorsal line, first at a limited space and then more completely till at last they form a closed medullary tube, wider anteriorly in its cephalic part, the whole thus giving rise to the primitive form of the brain and spinal marrow.

Below the medullary tube there is formed about the same time the cellular column named *chorda dorsalis* or notochord, which occupies the place of the centres of the future bodies of the vertebræ and basis of the cranium, and by a somewhat later process the rudiments of the vertebræ themselves in their centra or bodies, which enclose the notochord, and their neural arches which surround the medullary canal, together with the muscular plates, which are the source of the voluntary muscles, come to be developed from the middle layer.

The formation of blood-vessels and blood and the simultaneous development of the heart follow in another part of this layer, and in a somewhat later stage there take place the inflection and other changes of the whole blastodermic layers which mould the body of the embryo into a semblance of its later form, give the distinction of head, trunk, and limbs, and lay the foundation of the alimentary canal, its accompanying glandular

Fig. 638.

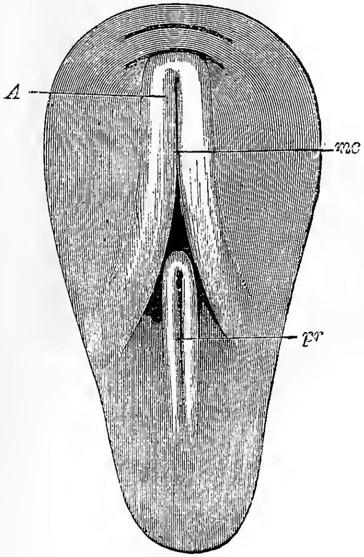


Fig. 639.

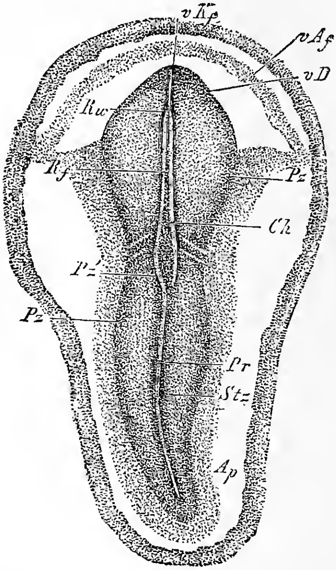


Fig. 638.—Surface view of the transparent area of a blastoderm of 18 hours, somewhat diagrammatic (from Balfour.)

pr, primitive groove, closed in front by the coalescence of the two lateral ridges; *mc*, medullary groove, having on each side the medullary folds or ridges A, which also meet in front to enclose the groove, but diverge behind so as to enclose the primitive streak; in front the fold of the amnion is commencing.

Fig. 639.—Area pellucida and rudiments of the embryo-chick of the second day. $\frac{19}{1}$ (From Kölliker.)

pr. primitive streak and groove; *Rw*, dorsal or medullary ridges meeting in front; *Rf*, medullary groove near its middle; *stz*, axial zone; *Pz*, parietal zone; *Pz*[1], two vertebral somites; *Ch*, notochord; *Vkf*, cephalic fold; *vD*, anterior intestinal fold shining through; *vAf*, anterior or amniotic fold; *Ap*, area pellucida.

and other organs, together with the extra-embryonic structures, such as the amnion, yolk-sack and allantois, constituting the coverings of the embryo and membranes of the developed ovum.

2. **Relation of the Layers of the Blastoderm to the Development of Different Systems and Organs.**—In this complex developmental process, according to the views of Remak, with such slight modification as is necessary to bring them into conformity with the results of more recent discovery, the upper layer of the blastoderm, which we name epiblast (or *neuro-epidermal*), is the exclusive source of the organs of the nervous system, central and peripheral, with the organs of sense, the

cuticular covering of the body and lining of the mouth, together with its accessory glands and other parts. The lower layer or hypoblast (the *epithelio-glandular*) gives rise to the epithelial lining of the alimentary canal and air-passages, the principal gland-ducts and the cellular elements of the glands.

Fig. 640.

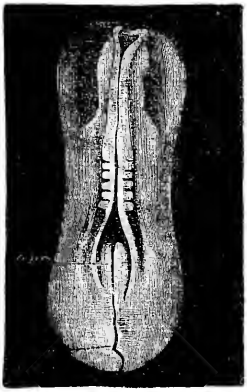


Fig. 640.—Dorsal view of a blastoderm and embryo chick having five mesoblastic somites (from Balfour).

a.pr, anterior part of the primitive streak; *p.pr*, posterior part; the medullary ridges have come together in the greater part of their extent, but have not yet united; the caudal swellings are visible on each side of *a.pr*.

The mesoblast undergoes subdivision and has a much more complex destination. By its inner column it forms the matrix of the cranio-vertebral skeleton and the associated voluntary muscles. By the upper plate of its lateral part (*Somatic or parietal Mesoblast*) it gives rise, in association with the epiblast, to the osseous, fibrous, muscular, and tegumentary substance of the body-wall and limbs; while its lower plate (*visceral mesoblast*), separated from the upper by the body-cavity, supplies the formative material for the fibrous and muscular wall of the alimentary canal, the lymph and blood-vascular system, and the urinary and generative organs.

The two divisions or plates of the mesoblast now referred to (parietal and visceral mesoblast) in extending themselves peripherally in the embryo and ovum, are more or less associated with the upper and lower layers, the upper with the epiblast, the lower with the hypoblast, so as to form two composite sheets of the blastoderm, the upper of which we shall name the *parietal or somatic wall*, and the lower the *visceral or splanchnic wall* (the Somatopleure and Splanchnopleure of Foster and Balfour, No. 30). Of these the upper gives rise by its inflection to the amnion

Fig. 641.

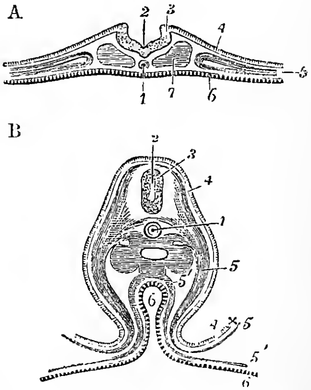


Fig. 641.—Transverse section through the embryo-chick before and some time after the closure of the medullary canal, to show the upward and downward inflections of the blastoderm (after Remak).

A. At the end of the first day. 1, notochord; 2, medullary canal; 3, edge of the dorsal lamina; 4, epiblast; 5, mesoblast divided into upper and lower plates; 6, hypoblast; 7, section of proto-vertebral somite.

B. On the third day in the lumbar region. 1, notochord in its sheath; 2, medullary canal now closed in; 3, section of the medullary substance of the spinal chord; 4, cuticular layer of epiblast; 5, somatic mesoblast; 5′, visceral mesoblast (one figure is placed in the body cavity); 6, hypoblast layer in the intestine and spreading over the yolk; 4 × 5, somatic wall going to form the amnion; 5′, 6, visceral wall passing into the yolk-sack.

or proper embryonic covering, which is continuous with the abdominal wall of the embryo at the umbilicus; while the lower sheet forms in its extension the greater part of two other membranes which are in direct continuity with the wall of the alimentary canal, viz., the yolk-sack and the allantois, all of which will be described later.

It requires to be noticed however that the foregoing account, though true of the great majority of mammalia, does not apply to them all. It has been long known, according to the discovery of Bischoff (No. 21, iv.), that in the guinea-pig the order of the position of the blastodermic layers is inverted in such a manner as to place the epiblast internally and the hypoblast externally, with a corresponding difference in the relative position of the parts developed from the several layers: and it has been recently shown by A. Fraser that a similar inversion of the layers exists in the rat and mouse. (Brit. Assoc. Aug. 1882.)

The existence of several laminæ in the germinal substratum was first suggested by C. F. Wolff in his celebrated work Theoria Generationis, published in 1759, and in his later Memoir on the Development of the Intestine first published in 1767 and republished in German by J. F. Meckel in 1812. It is, however, to the more exact researches of Pander, conducted under the direction of Döllinger of Würzburg, and published in 1817, and the modifications of them by Von Baer (1826-1837), that we owe the first consistent attempt to connect the development of the several organs and systems of the embryo with the different constituent parts or layers of the blastoderm. Pander recognised a trilaminar structure of the blastoderm and distinguished the three layers composing it, in their order from above downwards, or from without inwards in the egg, as the *serous*, *vascular*, and *mucous* layers (see Nos. 9, 10 and 12).

In 1850-54 a further important advance was made in the knowledge of the constitution of the blastodermic layers, by the discovery by Remak (No. 25) that the greater part of the middle layer soon after its formation comes to be divided into two laminæ, and separated by a space which corresponds to the perivisceral cavity—a fact which had been partially foreseen by Von Baer. So marked a division of the middle layer and distinction of the parts which are afterwards developed from its two laminæ, might seem almost to warrant the recognition of four distinct layers in the blastoderm; but it will be found on the whole more convenient to consider the fundamental layers as only three, to which, following the nomenclature of Foster and Balfour, we shall henceforth apply the designations of epiblast, mesoblast, and hypoblast, terms which are synonymous with those of ectoderm, mesoderm, and entoderm, employed by many authors.

3. **Origin and Constitution of the Blastodermic Layers.**—Returning now to the consideration of the constitution of the blastoderm, we shall find some difference of opinion prevailing among embryologists on this subject, and more especially as to the mode of origin of the middle layer. We cannot enter into a full discussion of this question here, but we shall endeavour to present a very brief view of the results of the most recent researches regarding it.

In the class of birds, as already noticed, the discoid blastoderm presents from the first, or from a very early period of incubation, a bilaminar arrangement of its cells, and there is no difficulty in identifying the greater part of the upper and more advanced layer with that which is afterwards known as epiblast. The lower layer consists at first of larger, more scattered and loose granular cells, but these or a part of them soon assume the more definite form of a distinct layer of flattened cells occupying the lowest place and therefore corresponding, according to most embryologists, to that which is later known as hypoblast. As yet there is no appearance of mesoblast or middle layer; but between

the eighth and twelfth hour of incubation in the fowl's egg, during which time the primitive streak has been formed, the blastoderm undergoes considerable change in connection with the development of the middle layer. The primitive streak consists in fact of a linear or strap-like

Fig. 642.

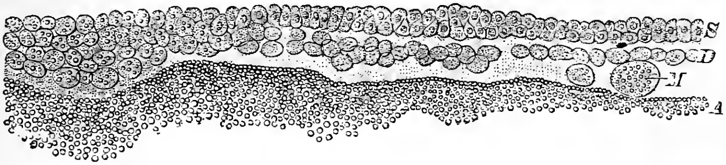


Fig. 642.—Microscopic view of a vertical section through half the blastoderm of a newly-laid egg. (From Stricker.) $\frac{230}{1}$

S, upper layer of small nucleated cells ; D, lower layer of larger granular cells ; M, segment spherules lying in the subgerminal cavity ; A, substance of the white yolk below the germ.

mass of cells, formed by direct proliferation from the lower cells of the epiblast, and continuing to adhere to that layer along the whole length of the streak. This is the axial plate of His and Kölliker, and, as first shown by the latter observer, is undoubtedly the commencement of a middle layer developed in connection with the epiblast.

At this time, that is, after the formation of the primitive streak and previous to the appearance of the medullary plates and chorda dorsalis, the blastoderm in the forepart of the germinal area, both of birds and mammals, consists of only two layers, and it is not till some time later that the mesoblast which gives rise to the protovertebral plates is found to have extended itself into this region.

Fig. 643.

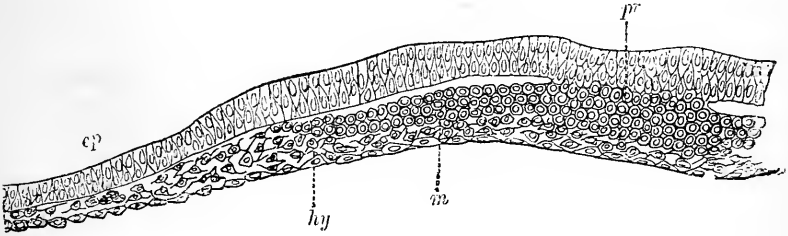


Fig. 643.—Transverse section through the front end of the primitive streak and blastoderm of the chick. (From Balfour.)

pr, primitive groove ; *m*, mesoblast ; *ep*, epiblast ; *hy*, hypoblast.

With regard to the much debated question of the mode of origin and extension of the mesoblast two different views mainly prevail among the embryologists who have most recently investigated the subject ; according to one of which, maintained by Kölliker (Nos. 28 and 99), Braun (No. 110) and others, the mesoblast is entirely derived from the axial plate of the

epiblast before referred to, and spreads from that source outwards into all the other parts of the embryo or ovum where it afterwards forms the foundation of new parts. According to the other view, held by Balfour (Nos. 32 and 96), His (No. 111) and others, while it is admitted that the mesoblast has the axial origin from epiblast before mentioned, it is maintained that there are probably two other sources from which it proceeds, viz., from the primary lower layer in the greater part of its extent, and from nuclei of the germinal wall of the yolk at its periphery.

Fig. 644.

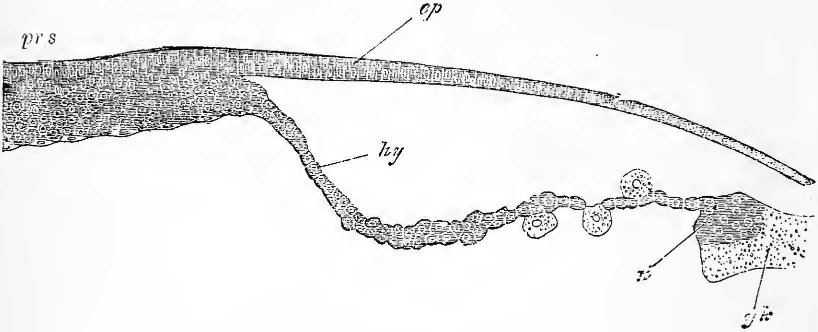


Fig. 644.—Longitudinal section of the blastoderm of the chick through the primitive streak and the part in front of it (from Balfour).

pr.s, primitive streak; *ep*, epiblast; *hy*, hypoblast in front of the primitive streak; *n*, nuclei in the yolk wall; *yk*, yolk.

In a recent revision of the whole evidence on this question as applied to birds, Balfour and Deighton (No. 108), founding their opinion upon new and very careful observations made by them on the common fowl and duck, state that after the lateral expansion of the layer of mesoblast formed in connection with the axial plate there takes place both in the region of the primitive streak and in the fore part of the germinal area a rapid proliferation of cells presenting a stellate character, and connected below with the upper surface of the lower layer over the whole extent of the transparent area. These cells are at first separate from the lateral parts of the axial mesoblastic plate, but below the primitive streak they are so intimately united with both epiblast and hypoblast as to render all three layers continuous in that situation. Balfour and Deighton therefore, while admitting with Kölliker the origin of a main sheet of mesoblast from the axial primitive streak plate, are inclined to differ from him so far as to attribute the origin of the lateral mesoblastic plates which form the mesoblastic somites in the region of the embryo to the differentiation of hypoblastic or lower layer cells, which however they allow are continuous with the wing-like or lateral extensions of the primitive streak or axial mesoblast. These authors further believe that a third set of mesoblastic elements may be derived from the peripheral portion of the blastoderm, viz., from the nuclei and cells of the germinal wall, from which elements the primitive blood and blood-vessels of the vascular area originate.

The latter view is one which has long been advocated by various embryologists, more especially by His (No. 29 and No. 111, i. and ii.), who in 1868 described the origin of the vascular as well as the connective tissues as taking place in the lower layer, and forming a special part of the mesoblastic elements under the name of *parablastic*. Similar views as regards the origin of the blood and vessels from peripheral blastodermic elements were brought forward by Peremeschko and maintained by Stricker and others of the Vienna school (Nos. 91 and 93).

In *mammals* the vesicular form of blastoderm, which results from the

holoblastic segmentation of the ovum, seems to determine some modification in the mode of formation of the layers. As already stated, the completion of the primary segmentation leads to the covering in of the whole ovum with a layer of flattened nucleated cells, within which,

Fig. 645.

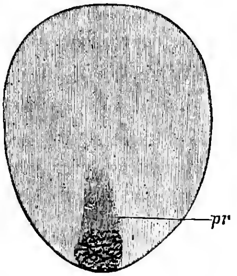


Fig. 646.

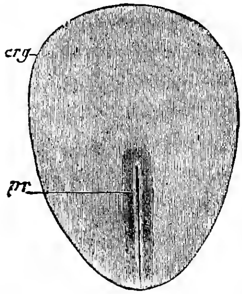


Fig. 645.—Embryonic area from the ovum of a rabbit of seven days. $\frac{30}{1}$. (From Kölliker.)

pr, first rudiment of the primitive streak.

Fig. 646.—Embryonic area from the ovum of a rabbit of eight days. $\frac{22}{1}$. (From Kölliker.)

arg, border of the embryonic area; *pr*, primitive streak with groove.

besides the fluid remains of the original yolk-substance, there is the inner mass of granular cells or segmental spheres, which by their further development and extension come to produce one or more deep or internal layers, which gradually spreading over the interior give a bilaminar or trilaminar structure to an increasing area of the blastoderm.

Fig. 647.

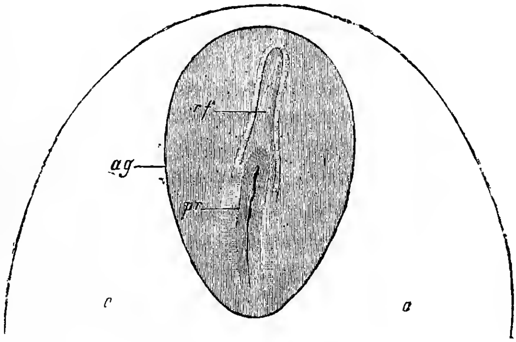


Fig. 647.—Embryonic area, with outline of part of the vascular area, from a rabbit's ovum of seven days $\frac{28}{1}$. (From Kölliker.)

oo, vascular area; *ag*, embryonic area; *pr*, primitive streak and groove; *rf*, medullary groove.

It is in the central part of the blastoderm, at the fifth day in the rabbit, and when the inner layer has advanced over about half of the interior, that a discoid thickening or opacity occurs which gives rise to

the *embryonal area* (*tache embryonnaire* of Coste); and it is now ascertained by the observations of Hensen, Kölliker and others, that the first appearance of the primitive streak and its groove and the commencement of the medullary canal and vertebral rudiments take place in a manner essentially the same as in birds. But the same or even a greater degree of doubt exists in mammals as in birds as to the mode of origin of the mesoblast, and there arises also in them the further question, viz., in how far the external vesicular layer of cells corresponds precisely to the later epiblast, as was for some time generally believed to be the case, or whether the deeper or internal layer of cells may also contribute to the formation of that layer.

Fig. 648.

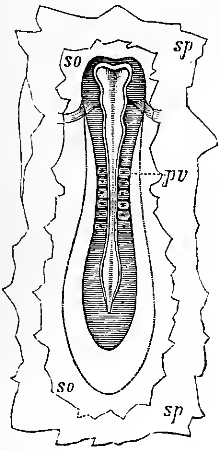


Fig. 648.—EMBRYO OF THE DOG SEEN FROM ABOVE, WITH A PORTION OF THE BLASTODERM ATTACHED.

The medullary canal is not yet closed, but shows the dilatation at the cephalic extremity with a partial division into the three primary cerebral vesicles; the posterior extremity shows a rhomboidal enlargement. The cephalic fold crosses below the middle cerebral vesicle. Six primordial vertebral divisions are visible; *so*, the upper division of the blastoderm; *sp*, the lower division, where they have been cut away from the peripheral parts.

Some part of the difficulty now mentioned has arisen from the observations of A. Rauber (No. 101), who in 1875 detected the presence, in addition to two other layers of the blastoderm in the rabbit, of a thin layer of flat cells closely adherent to the outer surface, which he found to have only a temporary existence, and gradually to disappear in the course of the development of the other layers. Lieberkühn a few years later (No. 104) showed that the outer layer of flat cells described by Rauber, which form the whole of the outer covering of the blastodermic vesicle resulting from the primary segmentation, is not the principal source of the permanent epiblast, but that that layer as well as the hypoblast or lower layer are the product of differentiation of the cells which form the internal mass of segmentation spheres or "yolk-rest."

Fig. 649.

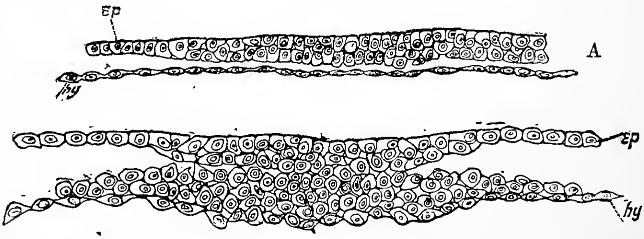


Fig. 649.—TWO TRANSVERSE SECTIONS THROUGH THE EMBRYONIC AREA OF THE RABBIT OF SEVEN DAYS. (From Balfour.)

A, through the anterior part of the embryonic area for about half its breadth; B, through the posterior part of the primitive streak; *ep*, epiblast; *hy*, hypoblast.

Kölliker, who was led by earlier observations on the blastodermic vesicle of the rabbit to coincide with the views of Rauber as to the transitory nature of the outer layer of flat cells, has more recently (1882) (No. 99, ii.) reviewed the

whole subject and has described the result of renewed observations made on the rabbit as follows :—

The embryonal area of the rabbit's blastodermic vesicle consists at the fifth day of three layers, of which the upper, corresponding to Rauber's flat cells, is the same with the outer layer of the primitive blastodermic vesicle, while the other two layers arise by the widening out of the mass of inner cells, and its subsequent division into two laminæ. The outer layer of cells is transitory, and is not the source of the permanent epiblast, which is formed, as Rauber supposed, from the upper of the two internal layers of cells, while the lower of these gives rise to the hypoblast. After the disappearance of Rauber's cells the blastoderm becomes for a time distinctly bilaminar, the cells of the upper layer being more regularly set

Fig. 650.

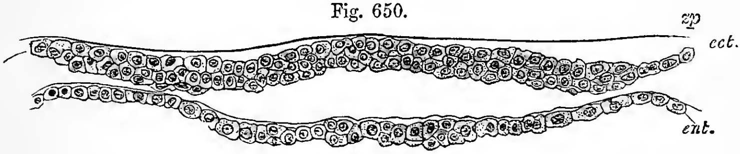


Fig. 650.—A SECTION THROUGH PART OF A BILAMINAR BLASTODERM OF THE CAT. (E. A. S.)

ect., *ent.*, ectoderm, entoderm ; *z.p.*, thinned out zona pellucida.

and columnar in form ; those of the lower being large and flat, as well described by Hensen (98) and Schäfer (No. 100).

The mesoblast first makes its appearance in the course of the seventh day in connection with the formation of the primitive streak, and according to Kölliker is formed entirely by proliferation of cells belonging to the epiblastic layer. This cellular multiplication takes place in an axial plate very similar to that previously described in the bird's egg, and the mesoblastic sheet which results extends in the

Fig. 651.

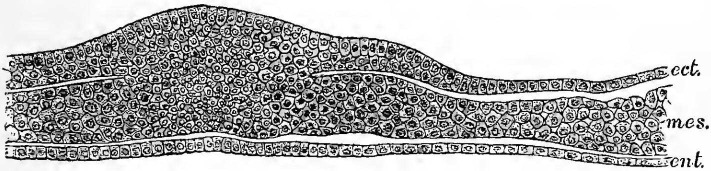


Fig. 651.—SECTION OF TRILAMINAR BLASTODERM OF THE RABBIT OF EIGHT DAYS AND NINE HOURS. (Kölliker.)

ect., *ent.*, as before; *mes.*, mesoderm continuous in middle (*pr.*) with ectoderm.

same manner forward along with the primitive streak from the margin of the embryonal area where their development begins.

According to Kölliker the cells of the mesoblast have from a very early period of their existence a marked spindle and stellate character, and in this respect differ obviously from those of the epiblast and hypoblast ; and thus the sheet of new formation is easily recognisable both on surface views and in sections, as it expands from its median attachment to the axial plate laterally over the surface of the germinal area. The sheet of mesoblast spreads out at first only to the sides of the primitive streak and backwards, being widest behind ; but after a time it also extends forwards in the form of two lateral plates which spread into the anterior part of the germinal area, in which previously the blastoderm was only bilaminar, and finally it passes from the embryonic area into the whole extent of the surrounding vascular area.

The observations of Heape, made like those of Lieberkühn upon the blastoderm of the mole, confirm those of Kölliker upon the rabbit in so far that

they show the larger portion of the mesoblast to be produced from epiblast in the axial plate of the primitive streak; but he is led by his researches also to advocate the view that a portion of the mesoblast is derived from hypoblast in the anterior region of the embryonal area in the same manner as Balfour holds to be the case in birds. He is also inclined to believe that the flat cells of Rauber combine in part with, or are converted into, the upper layer of the prismatic internal cells to form the epiblast (No. 107).

Fig. 652.

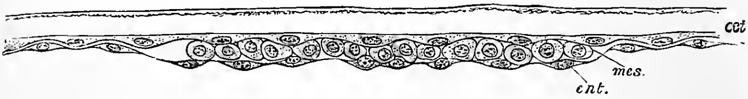


Fig. 652.—Section of the rabbit's blastoderm at six days. (From E. Van Beneden.)

ect., upper layer, or Rauber's cells ; *mes.*, middle layer ; *ent.*, lower layer.

E. Van Beneden takes quite a different view of these phenomena (No. 105). Not admitting the transitory nature of the upper layer as described by Rauber, he holds that this layer, which is co-extensive with the whole blastodermic vesicle, becomes the epiblast, that from the more restricted plate of deeper cells there is first formed a primitive lower layer, and that subsequently there takes place a separation or differentiation of this into a smaller central intermediate plate of rounded mesoblastic cells and a wider lower layer of flat hypoblastic cells (see fig. 652).

Fig. 653.

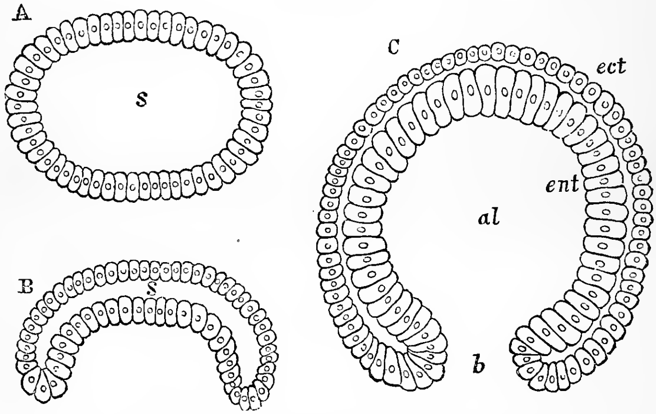


Fig. 653.—Ovum of amphioxus in the three stages of blastula, invagination and gastrula. (From Haeckel, after Kowalevsky.)

A. blastula stage, or single vesicular layer of cells resulting from segmentation ; B, invagination stage forming two layers ; C, gastrula stage in which a primitive alimentary cavity is enclosed by a bilaminar blastoderm ; *s*, segmentation cavity ; *ect.*, outer layer ; *ent.*, inner layer ; *al.*, primitive alimentary cavity formed by invagination ; *b*, blastopore.

GENERAL RELATIONS OF THE BLASTODERM TO THE OVUM.

Invagination of the Blastoderm, Gastræa Theory.—The brilliant discovery by Kowalevsky in 1867 (No. 83) of the production of a bilaminar condition of the blastoderm in Amphioxus and some invertebrate animals, by the infolding or invagination of a primary simple cellular blastodermic membrane (blastula) resulting

from the primary segmentation, and the attempt of Haeckel (No. 89) which followed to show that a somewhat analogous process is universal throughout all animals in which the distinction between ectoderm and entoderm exists, gave rise to an entirely new mode of viewing the relation of the blastoderm to the ovum and its embryonic development. In the Amphioxus the invagination consists in the doubling back or inwards of one half of the primary blastodermic vesicle upon the other, so that the two at last come into contact, by the gradual disappearance of the intervening cavity. At the same time the double wall thus produced bends round and converges at the margin of reduplication so as to enclose a new cavity which communicates with the exterior by a narrow aperture; this constituting the *gastrula* form of the developing ovum and embryo. The two layers forming the wall of this gastrula correspond with ectoderm and entoderm or the primary outer and inner layers of the blastoderm, and the now contracted aperture of invagination receives the name of blastopore appropriately given to it by Ray Lankester (No. 44). Now although it is very apparent that in the higher vertebrates, as well as in many of the lower animals, there is no actual infolding or invagination of the blastoderm such as that now described, yet there are circumstances connected with the origin of the layers, and their continuity at the place where the first traces of the embryo appear, which seem to make it possible to refer the phenomena of blastodermic and early embryonic development to a general principle in some degree consistent with the invagination and gastræa theories of Kowalevsky and Haeckel.

We cannot in this place enter upon the consideration of this extensive and difficult subject; but it may be proper to refer briefly to one or two points in connection with its history in the higher vertebrates as bearing upon these theoretical views.

Blastopore and Neurenteric Canal.—We have had occasion more than once to refer to the existence of the blastopore aperture or indications of it in the higher vertebrates. The more trustworthy of these indications are to be found entirely in the primitive streak and its groove, and in certain depressions and passages through the layers of the blastoderm which have been detected in their vicinity. It is more immediately in the space between the hinder extremity of the notochord and primitive medullary canal and the fore part of the primitive streak that in birds and reptiles the deepest aperture has been observed, in the form of a downward passage, which comes to be established some time after the formation of the mesoblast and protovertebral somites, and which leads from the exterior or from the hinder part of the still open medullary canal into the archenteron or primitive alimentary cavity round the hinder extremity of the notochord, and to which the name of *neurenteric canal* is given. The fact that the first development of a primitive trace takes place in all vertebrated animals at the margin, and not, as was formerly held, for the higher tribes, in the centre of the germinal area, affords some explanation of the very obscure relation subsisting between the outer and inner primary layers of the blastoderm, and opens up a way for the application of the theory of invagination to the early phenomena of development in the amniota as well as in the lower vertebrates.

In endeavouring to explain this matter we cannot do better than follow closely the able exposition of the subject given by Balfour, whose own researches have done much to demonstrate the applicability of the theory of invagination to the early development of the higher vertebrates. A careful consideration of the relations of the primitive trace and its groove to the ovum and earliest phenomena of development, its transitory existence as discovered by Dursy in 1867 (No. 90), the occasional perforation of the layers of the blastoderm in a part of it, and its intimate connection with the origin of the mesoblast, has led Balfour, and after him several other embryologists, to the view that the primitive trace is the vestige of a blastopore or aperture of invagination of the blastoderm, and that its groove and prolongation as a trace arise from the very early and rapid extension of the blastoderm round these structures.

In illustration of this subject we may refer to the diagram contrived by Balfour, to show the relations between the medullary groove, the primitive trace, and the rest of the blastoderm in three different forms of development as presented by the Amphibia, the Elasmobranchs, and the Amniota.

We shall suppose that in all the three sets of animals here referred to, the primitive blastoderm already consists of two layers or groups of cells, viz., an external epiblastic, and a deeper or internal set representing the primitive hypoblast, and (leaving in the meantime the mesoblast out of view) supposing further that the outer layer or epiblast has to a greater or less extent covered in the deeper layer, there is seen in A, which represents the frog's ovum, a round spot, *yk*, where the inner larger cells or yolk spheres are still exposed, and at *ne* a depression where the outer and inner cells are continuous. These together represent the blastopore or place of invagination; and it will be seen further that it is at this point and from it forwards, that is towards the head end of the embryo,

Fig. 654.

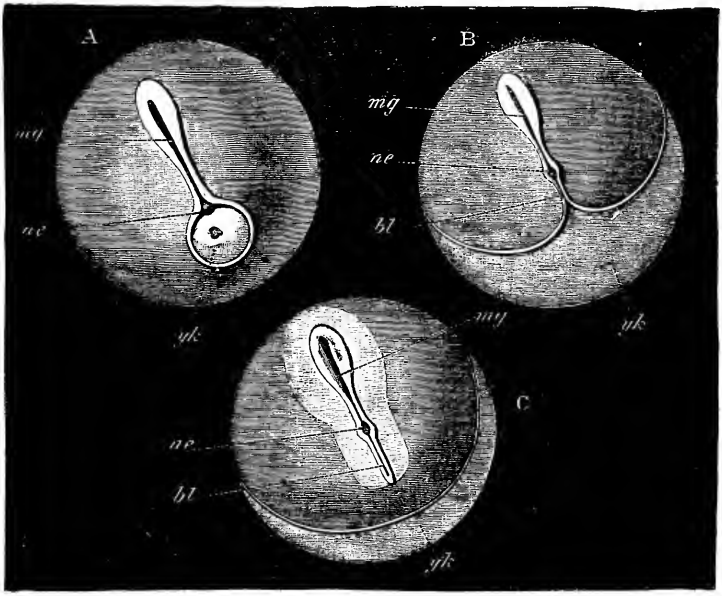


Fig. 654.—DIAGRAMS ILLUSTRATING THE POSITION OF THE BLASTOPORE, AND THE RELATION OF THE EMBRYO TO THE YOLK IN VARIOUS MEROBLASTIC VERTEBRATE OVA. (From Balfour.)

A, type of the Frog; B, elasmobranch type; C, amniotic vertebrate; *mg*, medullary plates and groove; *nc*, neurenteric canal; *bl*, portion of blastopore adjoining this canal; *yk*, part of yolk not yet enclosed by the blastoderm; in B and C, *bl* is the seat of the primitive streak.

that the medullary canal, *mg*, is developed. By the extension of the outer layer the round spot, long known as the anus of Rusconi, is covered gradually over by the epiblast, and the aperture of invagination reduced in size, is finally closed; the neurenteric canal being left, however, for a time more deeply. The permanent anus is of later formation.

In the elasmobranch fishes (B), of which the ovum is meroblastic, the blastoderm is seen to have extended only a certain way over the yolk, but in such a manner as to involve or surround the blastopore aperture, which may be supposed to have been previously marginal or at the union of the outer and inner blastodermic layers, and thus to give rise to a prolongation of the aperture in the form of a groove, *bl*, by the meeting of the blastoderm from the two sides.

In the amniota, C, the separation of the embryonic area still further from the margin of the blastoderm is effected by the rapid extension of the latter beyond

the aperture of invagination, and thus the blastopore and its prolongation as a primitive trace and groove are brought more fully within the embryonic area, while the medullary groove stands in the same relation as in the lower animals. It will be seen, however, that the first indication of the primitive trace even in the amniota arises marginally, and it is probable therefore that it essentially corresponds in position with that of the lower vertebrates.

From this it appears that the first traces of embryonic formation in these several groups of animals stand in a constant and determinate relation to the blastopore, or if we do not go so far as to admit the occurrence of actual invagination, to the place of continuity between the upper and lower primary layers of the blastoderm, and to the seat of primary differentiation of the principal part of the mesoblast.

Fig. 655.

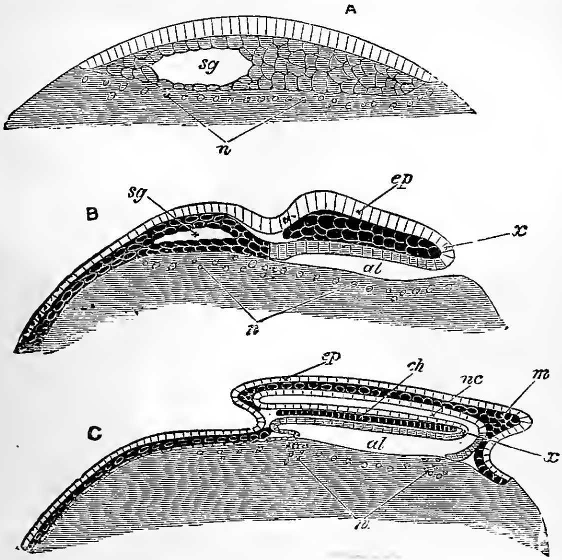


Fig. 655.—Diagrammatic Longitudinal Sections of Elasmobranch Embryo and Blastoderm. (From Balfour.)

A, younger stage with two primary layers ; B, more advanced stage with three layers and invagination at the hinder end of the embryo ; C, still more advanced ; the embryo raised from the blastoderm with neural and primitive alimentary canals and neurenteric communication between them.

ep, epiblast ; *m*, mesoblast ; *x*, epiblast continuous with hypoblast ; *nc*, neural canal ; *ch*, notochord ; *al*, alimentary cavity ; *sg*, segmentation cavity ; *n*, nuclei of the yolk.

It may be proper to make mention here of the remarkable observation by E. Van Beneden of the existence of a small aperture or deficiency in the external layer of cells on that side of the rabbit's ovum where the inner cells or segmental spheres (forming the yolk-rest) adhere to the outer, which appeared to him to have the effect of establishing continuity between the outer and inner layers of the blastoderm in the manner of a blastopore. But there are difficulties in the way of reconciling this view of a mammiferous blastopore with those of Balfour and others on this subject as founded on the observation of invagination in the lower vertebrates. (See No. 75.)

The existence of a neurenteric canal or blastopore in birds was discovered by Gasser in 1879 (No. 103), and has been confirmed by Balfour and Braun ; and from these observations it appears that it is subject to some variation in position and extent in that class of animals.

This discovery was extended to the class of Reptiles (Lizards) by Kupffer and Benecke in 1879 (No. 112), and confirmed by original observations by Balfour; and a further series of researches by Kupffer (No. 113) in the present year, have shown that the neurenteric canal exists in Ophidia and Chelonia.

We owe to Hensen the first clear account of the development of the primitive streak in mammals (rabbit), and his observations have been ably followed up by Kölliker. The observations of Schäfer on the early blastoderm of the guinea-pig have shown more clearly the connection subsisting between the lower

Fig. 656.

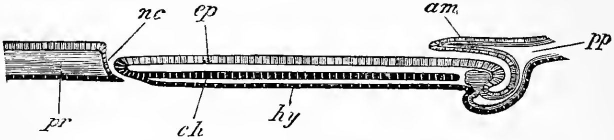


Fig. 656.—Diagrammatic Longitudinal Section of an Embryo of Lacerta. (From Balfour.)

pp, body cavity; *am*, amnion fold; *nc*, neurenteric canal; *ch*, notochord; *hy*, hypoblast; *ep*, epiblast of the medullary plate; *pr*, primitive streak. In the primitive streak all the layers are partially fused.

layer in the medullary or embryonic region and the epiblast and mesoblast in the anterior extremity of the primitive streak, and according to Balfour a comparison of this with the conditions observed in reptiles and birds leaves little doubt that this union may be looked upon as the dorsal lip of a blastopore. In the mole (and partially also in the rabbit) Heape has ascertained the existence of a neurenteric canal similar to that observed in other vertebrates (No. 107). This appears first as a pit at the anterior extremity of the primitive streak, and in later stages perforates the floor of the hinder end of the medullary groove. A. Fraser also has seen the neurenteric canal in the rat.

Direction of the Embryonic Axis.—It is well known that in the common fowl and other birds the line of the primitive streak continued through the

Fig. 657.

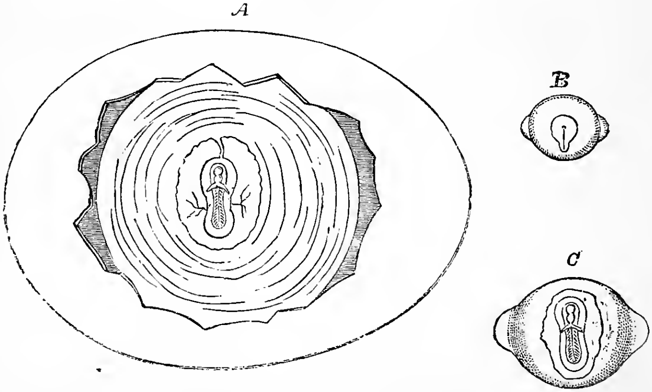


Fig. 657.—Outlines showing the relation of the axis of the embryo to the ovum in birds and mammals. (A.T.)

A, Fowl's egg opened after 35 hours' incubation, showing the embryo chick within the transparent and vascular area on the surface of the yolk; at right angles to the long axis of the egg; B & C, two early stages of development in the ovum of the dog, showing the primitive streak (in B) and the commencing embryo (in C); the line of the uterine tube and long diameter of the ovum being at right angles to the vertebral axis of the embryo.

medullary groove which represents the vertebral axis of the embryo is during the first two days of incubation always placed at right angles to the long axis of the egg, and in a determinate position, so that if one looks down upon the germinal area in an incubated egg the small end of which is placed towards the right hand, the cephalic extremity of the embryo is directed forwards, and the caudal extremity and primitive streak backwards.

There is some reason to believe that the line of the first cleavage of the germinal area may be the same with that of the first embryonic axis as now described both in birds and amphibia, but this is not fully known. It deserves to be noted, however, that the position of the cicatricula in the yolk or ovarian egg is also fixed, being invariably close to the pedicle of the ovicapsule, and all this seems to indicate some constant relation between the position of the egg, the mode of cleavage, and the attitude of the first lineaments of the embryo.

In mammals also numerous observations show that the axial line of the embryo is constant, and is placed so as to cross the long axis of the uterus, as may be seen in the dog, pig, sheep, rabbit, rat and guinea-pig. But in both mammals and birds this first determinate position is soon lost, and a more variable one is assumed by the embryo when its development has advanced so as to separate the body from the rest of the blastoderm by an umbilical constriction. The cause of these relations of position is still entirely unknown.

III. SPECIAL HISTORY OF THE DEVELOPMENT OF THE OVUM.

In the ova of the higher vertebrates the phenomena of development fall naturally into two groups, according as—1st, they occur in parts belonging strictly to the body of the future embryo, and are therefore embryonic; or 2nd, they are connected with the production of parts which being situated external to the body of the embryo may be regarded as accessory and called extraembryonic. We shall begin with the second of these divisions as affording a convenient opportunity of explaining some general relations of connection between the embryo and the other parts of the developing ovum.

I. DEVELOPMENT OF EXTRAEMBRYONIC PARTS.

Membranes of the Ovum in General.—In the three higher classes of vertebrates the extraembryonic structures consist of the membranes named yolk-sac, amnion and allantois; and to these may be added a fourth, existing only in mammals, and which may best be named the chorion. We shall first state the most general facts as to the development of the membranes; and then in connection with human uterogestation describe the formation of the placenta, which is the organic medium of connection between the ovum with its embryo and the maternal uterus.

It is to be noted that this description will not apply to many of the phenomena observed in the exceptional forms in the guinea-pig, rat and mouse.

The Yolk-sac.—This name is given to an organised and vascular covering formed by the extension of the layers of the blastoderm over the surface of the yolk, and existing in all vertebrate animals.

The yolk-sac is the seat of the first circulation of the blood in the vitelline or omphalo-mesenteric vessels of its vascular area, and in oviparous animals especially these vessels spread at a later period over the whole surface of the yolk in the membrane which forms the sac. In birds the food-material of the yolk is absorbed by these vessels and

conveyed by them as nourishment into the system of the embryo, through a special structural arrangement of the membrane, which is thrown into folds and beset with tufted groups of cells surrounding the vessels of its interior. (Courty, in Ann. d. Sc. Nat. 1844.)

In mammals as in birds the vascular area spreads over the surface of the yolk, but does not in all cover it entirely. In some the yolk-sac grows with the embryo and other parts of the ovum to a large proportional size, which it retains up to an advanced stage of development, while in others its growth ceases at an early period, and this is followed in some by the atrophy and complete disappearance of the yolk. The cavity of the yolk-sac is in most occupied chiefly by a coagulable fluid without the peculiar yolk corpuscles which belong to the yolk-substance of birds and reptiles.

The differences which are observed in the extent of development of

Fig. 658.

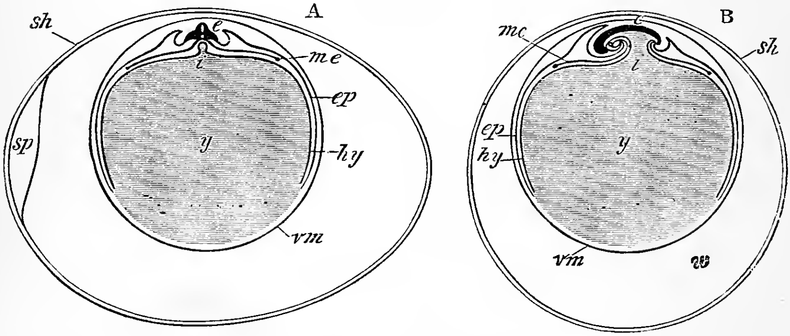


Fig. 658.—Vertical sections of an incubated fowl's egg, longitudinally and transversely, at the third day.

The figure is diagrammatic and is intended to show the early relations of the membranes to the embryo and rest of the egg. The parts of the embryo and those near it are represented as proportionally larger than natural. A, longitudinally in the egg, and across the embryo ; B, across the egg and longitudinally in the embryo ; *sh*, shell and external covering of the egg ; *sp*, air space at the larger end ; *y*, the yolk partially covered by the spreading layers of the blastoderm, viz., *ep*, epiblast, *hy*, hypoblast, and *me*, visceral mesoblast as far as the vascular area extends ; *vm*, vitelline membrane ; *w*, space occupied by the albumen of the egg ; *e*, the embryo (shaded dark) consisting of its medullary and protovertebral axis, and partially surrounded by the commencing folds of the amnion in connection with epiblast (*ep*) ; *i*, the place of communication of the primitive intestine with the yolk-sac. For the sake of clearness the parietal mesoblast has been omitted.

the yolk-sac and its blood-vessels may be traced to differences in their relation to the chorion in utero-gestation. In rodentia, and to some extent also in insectivora and cheiroptera, it comes into contact or union with the non-placental part of the chorion, and furnishes blood-vessels to that membrane. In ruminants it is very soon drawn out into two attenuated tubes which extend towards the ends of the greatly-elongated ovum. In carnivora it is of considerable size, stretching through the ovum towards its opposite poles, but without vascular union with the chorion.

In the human species the yolk-sac, which is also named the umbilical vesicle, retains its vascularity for a short time, and continues to grow up to the fifth or sixth week, at which time it has assumed a pyriform shape, and is connected by a tubular vitelline duct with the intestine.

In an ovum of from five to six weeks it is about a quarter of an inch in diameter, and lies loosely in the space between the amnion and chorion. At a later period, the duct elongating with the umbilical cord, the vesicle remains flattened and atrophied in the same relation to these membranes as before. In the third month its duct is found connected with a coil of intestine which in the form of a hernia occupies the umbilical cord outside the abdomen of the embryo (see fig. 789, p. 882). At a later period the much elongated and attenuated duct with the vitelline vessels, now shrunk and impervious, may still be traced through the umbilical cord, while the flattened vesicle may be found even up to the end of the term of uterogestation.

The Amnion.—This vesicular covering of the embryo does not exist in amphibia or fishes, but is present in all reptiles, birds, and mammals,

Fig. 659.

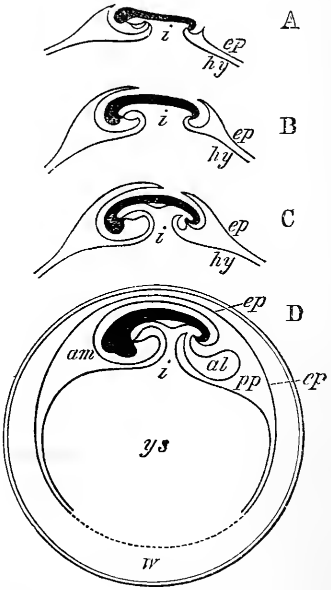


Fig. 659.—Diagrammatic outlines of longitudinal sections of the embryo-chick at successive periods during the formation of the membranes. (A. T.)

A, at the beginning, B, towards the end of the second day of incubation; C, on the third day; D, on the fourth day, showing also a section of the whole egg. In all these figures the embryo and the neighbouring inflections of the membranes are represented proportionally larger than natural. The dark-shaded part indicates the embryo: *ep*, epiblast; *hy*, hypoblast; (for the sake of clearness the mesoblastic folds accompanying these are not represented). In A, the cephalic fold of the amnion has begun; in B, it has increased, and the caudal fold has commenced; in C, the two folds approach one another, leaving the amnion still open dorsally; in D, the outer fold or false amnion has separated from the inner or true amnion which is now complete; *ys*, the cavity of the yolk being gradually surrounded by the yolk-sac formed of all the three layers of the blastoderm, and communicating at *i*, with the alimentary canal; *al*, in D, shows the allantois beginning to expand from the intestine; in C, it is just beginning to appear.

which are hence named *Amniota.* It begins to be formed at an early stage of development, and subsequently becomes distended by a fluid in which the embryo floats and is attached by means of the umbilical cord to its amniotic enclosure.

The structure and mode of formation of the amnion are essentially similar in the three classes of animals in which it exists. It generally consists of two layers, derived respectively, the inner from the epiblast, and the outer from the parietal layer of the mesoblast; the first formed of distinct nucleated cells, the second presenting in later stages a fibrous structure. The external layer possesses considerable muscular contractility and in some animals is partially vascular.

The formation of the amnion takes place by the gradual inflection in a dorsal direction from the flat part of the blastoderm adjoining the embryo of the two layers before mentioned, first at the cephalic, and

somewhat later at the caudal extremity and at the sides (see fig. 659, A, B, C and D), so that the two layers of which the amnion is composed are lifted up and separated from the remaining two lower layers (visceral mesoblast and hypoblast) of the blastoderm, by a space which is a peripheral extension of the pleuro-peritoneal cavity. The embryo thus comes to sink into a hollow produced by the rising of the amniotic folds round it. The backward folds deepening more and more, gradually converge on the dorsum of the embryo, and at last come together, the margins of the reflection narrowing rapidly and being finally completely obliterated or lost by their convergence and by the subsequent dissociation of the inner from the outer divisions of the folds (fig. 659, D). The separated inner division now becomes the entire closed sac of the amnion, connected only with the rest of the parts at the umbilical constriction where it is continuous with the integument of the embryo. The outer dissociated division is the *false amnion* of Pander and Von Baer, passing out into the peripheral part of the blastoderm, and constituting for a time an external covering of the ovum, which in birds and reptiles appears afterwards to be lost by thinning or absorption; but which in mammals is probably connected with the development of the permanent chorion in a manner to be referred to hereafter.

In birds at a more advanced stage of incubation the true or enclosed amnion is surrounded externally by the expanded allantois. In mammals its relations vary somewhat according to the nature and extent of the proportional development of the yolk-sac and allantois. In the advanced stage of the development of the human ovum the amnion is to a great extent in contact with the interior of the chorion; but its origin and formation do not differ materially from those of animals.

In the human embryo, as in that of most animals, the amnion is at first and for some time after its completion very close to the surface of the body, but after a time, corresponding to the fourth day of incubation in the chick and the fourth or fifth week of gestation in man, the increased accumulation of fluid within the amnion expands the membrane rapidly so as to remove it to a considerable distance from the embryo.

The muscular contractility of the amnion doubtless resides in its outer layer derived from the parietal mesoblast. The contractions appear to be rhythmic, and they may be seen in the opened incubated egg of the fowl, or even in the entire egg, by means of a bright light in a dark chamber, from the sixth or seventh day of incubation; and it is probable that they are of a similar nature in mammals.

The human amniotic fluid contains about 1 per cent. of solid matter, consisting chiefly of albumen, with traces of urea, which is probably derived from the urinary secretion of the fœtus.

It would appear that there is a difference in the structure of the reflected or false amnion in birds and in mammals. In the former it is composed of the same two layers as the amnion itself, their position being reversed, but in mammals the development of the mesoblast appears to cease at the place of reflection of the true into the false amnion, so that the latter consists only of the epiblast.

The Allantois.—This membrane, sometimes also called urinary vesicle, exists as a fœtal structure in all the amniota, but not in fishes or amphibia; and yet in the latter animals a corresponding vesicle is developed in the adult. In reptiles, birds, and mammals it originates at a very early period as a diverticulum from the hinder part of the primitive

intestine, but there are great differences in the degree and rate of its extension, a rapid and wide expansion occurring in some, while in others it remains of comparatively small size. It is the seat of an extended distribution of ramified and capillary blood-vessels which perform important functions in connection with the nutrition of the embryo and the aëration of its blood.

The allantois at its origin consists essentially of a thickened bulging portion of the visceral mesoblast, and a corresponding extension of the intestinal hypoblast within; and from recent researches in reptiles (Kupffer No. 113) would appear to have close relations with the neurenteric canal. The capillary network of commencing blood-vessels makes its appearance in its mesoblastic layer at a very early stage, and these become connected with the main vessels of the embryo by means of two

Fig. 660.

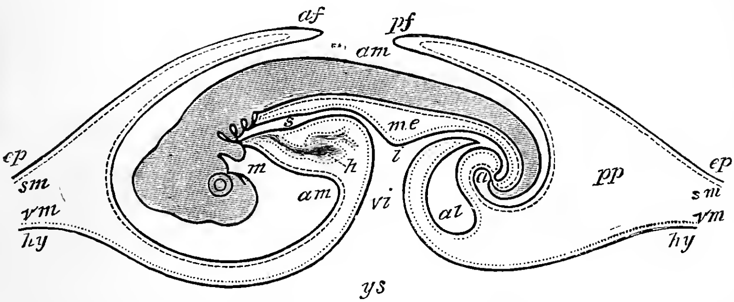


Fig. 660.—Enlarged diagrammatic outline of a longitudinal vertical section of the chick and neighbouring parts of the blastoderm on the fourth day. (A. T.)

ep, epiblast; *sm*, parietal mesoblast, together forming the *somatic plate; hy*, hypoblast; *vm*, visceral mesoblast, together forming the *visceral plate; af*, cephalic fold; *pf*, caudal fold of the amnion; *am*, cavity of the true amnion; *ys*, yolk-sac, leading by *vi*, the vitello-intestinal aperture to *i*, the intestine; *s*, the stomach and gullet; *a*, the future anus still closed; *m*, the buccal cavity or mouth formed in epiblast and still closed from the pharynx at the fauces, which are not shown; *me*, the mesentery; *al*, the allantoid vesicle communicating by its pedicle with the hinder intestine; *pp*, the space between the outer and inner folds of the amnion, which is an extension of the body cavity or pleuro-peritoneal space within the embryo between the parietal and visceral mesoblasts. The shaded part of the figure represents the head and trunk of the embryo in which the eye and the jaws with the branchial bars and clefts are indicated. The epiblast and hypoblast are drawn with entire lines, the parietal mesoblast with an interrupted and the visceral mesoblast with a dotted line.

arteries and two veins. The allantoic arteries are at first separate branches of the two primary divisions of the abdominal aorta, and subsequently, when the two aortas coalesce, they are derived from the hypogastric arteries, and have been called umbilical. The two returning vessels or allantoic veins pass into connection with the principal veins of the yolk-sac, and with them form the umbilical veins. The name of allantoic suggested by Balfour is preferable to that of umbilical for the vessels of the allantois.

The allantoid diverticulum soon takes the form of a flask-like vesicle, connected with the intestine by a narrow pedicle, as may be well seen in the chick on the fourth day, and in the embryo of the rabbit

or dog at a corresponding period. In all birds, as also in reptiles, it undergoes rapid dilatation and extension, and its inner hypoblastic portion being filled with fluid, and the doubled membrane flattening out in the space which intervenes between the parietal and visceral mesoblast, as far as is allowed by the separation of these two layers, viz., to the margin of the vascular area of the yolk, it follows the gradual extension of that area over the surface of the yolk; and finally, as the albumen gives place by its absorption into the yolk cavity, the allantois comes to occupy more and more of the intermesoblastic interval, and to fill the whole space between the amnion and yolk-sac on the one hand and the lining membrane of the egg shell on the other.

The allantoic blood-vessels are distributed both in its internal and external folds, but form a richer network on the latter, and there they

Fig. 661.

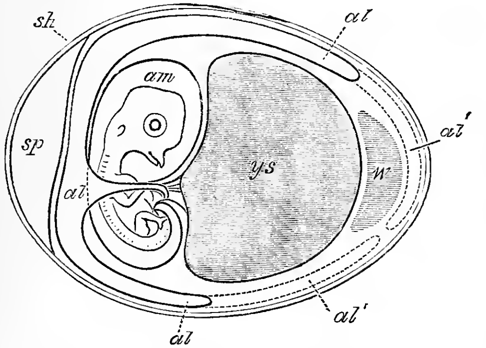


Fig. 661. — Diagrammatic outline of a longitudinal section of the fowl's egg about the middle of incubation. (A.T.)

sh, the shell and its membrane; *sp*, the air space much enlarged; *am*, the amnion with the enclosed embryo now placed towards the large end of the egg and air space; *ys*, the yolk and yolk-sac; *al*, the allantois expanded as a doubled vesicular membrane over a considerable part of the internal surface of the egg; *al'*, in dotted lines indicates the manner in which its expanding folds will ultimately meet and cover the whole of the deeper parts; *w*, the hardened remains of the white or albumen which towards the end of incubation lie between the yolk-sac and the allantois.

exhibit in the arteries and veins a marked difference of colour which indicates the action of the air upon the blood through the egg-coverings analogous to that of a respiratory organ.

It is also worthy of notice that from the time when the allantois has attained some size, it, like the amnion, is possessed of contractility, which resides in its mesoblastic layer; and accordingly on opening an incubated egg, from the effect of change of temperature or other stimuli, active motions may be perceived, caused by the alternate contraction and relaxation of different parts of the membrane.

In some of the mammalia the origin and early development of the allantois is nearly the same as in birds, but in a more advanced stage of development the relations of this membrane to the other parts of the ovum are greatly modified by its combination with the chorion, more especially in the region of the placenta.

In most mammals the external or mesoblastic lamina of the allantois undergoes greater extension than the inner hypoblastic sac, and this is remarkably the case in the human subject, in which it is still doubtful whether any internal vesicle is present beyond the limits of the umbilical cord. In the human ovum the external or mesoblastic vascular element probably spreads at a very early period over the whole interior of the chorion (placental and non-placental parts), while the internal or hypo-

blastic vesicle either shrinks and atrophies at a very early period or is comparatively small and has never reached the interior of the chorion. This subject will again be referred to in the account of human utero-gestation.

Fig. 662.

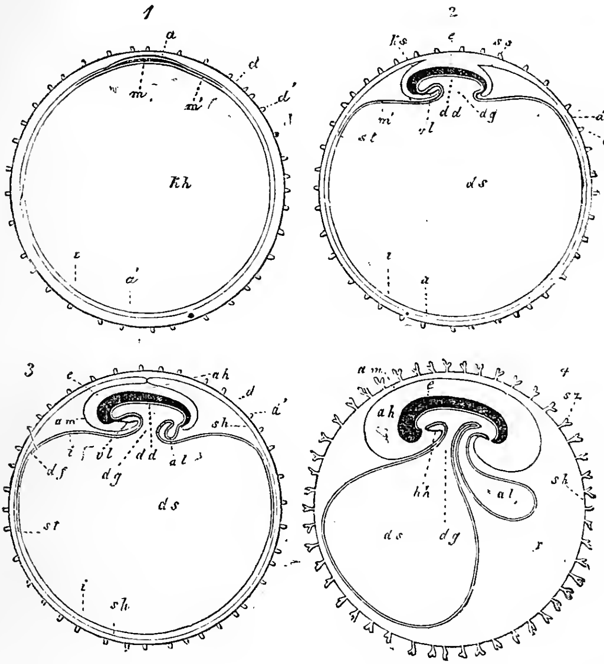


Fig. 662.—DIAGRAMMATIC SECTIONS OF THE MAMMIFEROUS OVUM IN DIFFERENT STAGES OF DEVELOPMENT TO SHOW THE PROGRESS OF FORMATION OF THE MEMBRANES. (From Kölliker.)

1. Ovum in which the chorion has begun to be formed, with the blastoderm and rudiment of the embryo within. 2. Ovum in which the cephalic and caudal folds have contracted the umbilical aperture towards the yolk-sac, and the amniotic folds are turning towards the dorsal aspect. 3. The amniotic folds being completed have met in the dorsal region; the umbilical opening is more contracted, and the allantois has begun to sprout. 4. The true amnion is detached from the reflected or false amnion which has disappeared or combined with the chorion; the cavity of the amnion is more distended; the yolk-sac is now pediculated, the allantois projects into the space between amnion, chorion, and yolk-sac, and the villi of the chorion begin to ramify.

d, external membrane or primitive chorion; *d′*, commencing villi of the chorion; *sh*, subzonal membrane or chorion; *sz*, villi of the chorion more advanced; *am*, amnion; *ah*, its cavity; *ks*, cephalic fold; *ss*, caudal fold of the amnion; *a*, the embryonal rudiment in the epiblast; *m*, that in the hypoblast, and *m′*, in the mesoblast; *st*, margin of the vascular area in its early stages; *dd*, hypoblast; *kh*, hollow of the vesicular blastoderm, becoming afterwards *ds*, the hollow of the yolk-sac; *dg*, ductus vitello-intestinalis; *al*, allantois; *e*, embryo; *r*, original space between amnion and chorion; *vl*, wall of the thorax in the region of the heart; *hh*, pericardial cavity.

The urinary bladder of mammals is produced by a dilatation in the pedicle of the allantois near the cloaca and within the body of the embryo. The urachus is the tubular extension of the walls of the bladder towards and in part through the umbilicus to join the allantois,

but the extent to which its hollow is prolonged varies greatly among animals, and in the human embryo this does not in general pass beyond the root of the umbilical cord.

The Chorion.—Under this name there has been long known in human embryology a most characteristic but rather complex membrane which surrounds the ovum from the earliest period at which it has been observed within the cavity of the uterus, and which probably begins to be formed about the ninth or tenth day after conception. This is the villous or shaggy vascular chorion, a part of which takes an important share by its further development in the formation of the fœtal portion of the placenta, while the remainder may be recognised as persistent during the whole of uterogestation.

An external covering of the ovum having a very similar origin and structure, and with analogous relations to the other parts, exists for a time in all mammals, and though in many less developed and less persistent than in the human ovum, still deserves the same name.

The mammiferous ovum when it enters the uterus has still a covering from the ovarian zona pellucida, but in the rapid expansion which the blastodermic vesicle undergoes within the first or second day after the completion of the segmenting process, the zona seems either to be much attenuated and finally lost, or may possibly be combined with the outer layer of the blastoderm, which then surrounds the whole ovum. In some animals, such as the rabbit, dog, and cat, and the same is probably the case in man, previous to the appearance of any trace of the embryo, but when an embryonic area may have been formed, villi begin to project from the surface of the ovum, and from the primitive cellular structure of the villi it is almost certain that they proceed from the outer layer of the blastodermic vesicle, to which therefore must be mainly attributed the first origin of the chorion. These villi extend over a large portion of the surface, perhaps only excepting the embryonic area and a part of the ovum where it is not in contact with the uterine wall. They are at first destitute of blood-vessels and are of simple cellular structure. They soon become pervaded in their interior by connective fibro-nuclear tissue derived from the mesoblast, which extends itself below the primitive epiblast. Some time later or after the development of the vascular membranes of the yolk and allantois, and after the completion of the fold of the amnion and the separation of the false amnion, the villi acquire blood-vessels which penetrate the connective tissue of their interior, and are in some animals wholly, in others partially derived from those of the allantois ; in the latter case, as before stated, the chorion receives blood-vessels also from the yolk-sac.

In birds the separation of the parietal and visceral mesoblast, and the intervention of the allantois between them, leads to the formation of an external membrane, composed of epiblast and parietal mesoblast, which lies close to the outer covering of the egg ; but this membrane afterwards unites with the visceral mesoblastic layer of the allantois and thus loses its independence.

In mammals, however, this external membrane formed of the false amnion and its peripheral continuation in the blastodermic vesicle constitutes the basis of the chorion, and is the same as that to which Turner proposes to give the name of *subzonal membrane.*

The further history of the development of the chorion will be given in connection with the formation and structure of the placenta, but

previously to entering upon that subject, it will be proper at this place to give some account of the early development of the human ovum and embryo.

HUMAN UTEROGESTATION.

1. **Early Stages of the Human Ovum.**—Great obstacles have stood in the way of the study of the earlier stages of the development of the human embryo and its membranes from the extreme rarity of the opportunities for observing the ovum in perfectly natural conditions within the uterus after death, and from the frequency of abnormal changes in aborted products in the first two months of pregnancy. Within the last few years, however, some important contributions have been made to the knowledge of this subject, among which is deserving of special notice the elaborate Monograph, by Professor His, in which much new information is supplied and the first systematic attempt has been made to investigate the human embryo by the method of sections (No. 132, 1880–82).

The impregnated ovum has never been detected in the course of its descent through the Fallopian tubes of the human female. From the analogy of animals and some observations on the changes in the uterus it is believed that the human ovum may arrive in that cavity at the seventh or eighth day after impregnation, but although instances are recorded in which at the eighth day a delicate vesicular body was found partially imbedded in the inner wall of the uterus, which from the probability of impregnation having taken place might possibly be an ovum, yet these bodies were not observed with sufficient accuracy to determine their nature, and it does not appear that the human ovum has been with certainty distinguished in the uterus before the tenth or twelfth day.

In a certain number of such observations the ova were found to have attained the size of a small pea or nearly a quarter of an inch in diameter, and were already more or less beset with villi on the outer surface of the chorion; no embryo was to be seen in these cases, nor such a structure of the membranes as to make it probable that the process of embryonic development had made any advance.

Fig. 663.

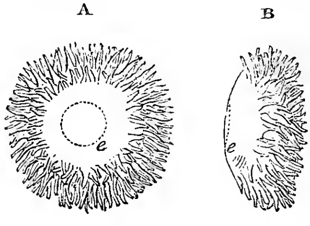


Fig. 663.—Front and side views of an early human ovum four times the natural size (from Reichert).

This ovum is supposed to be of thirteen days after impregnation. The surface bare of villi is that next the wall of the uterus, showing at *e*, the opacity produced by the thickened embryonic disc. The villi covered chiefly the marginal parts of the surface.

One case of this kind deserves especial notice from the very favourable circumstances under which it was examined (Reichert, 1873, No. 125). It was found in the uterus of a woman who committed suicide, and from the facts known as to her history it was believed by Reichert to be of twelve or thirteen days after conception. Its largest diameter was 5·5 mm. Its shape was that of a flattened spheroid, and the simple villi which partially beset its surface extended mainly over the equatorial margins, and left the two flatter surfaces bare to the extent of 2·5 mm.,

or $\frac{1}{10}$th of an inch. No traces were anywhere to be detected of an embryo; but the membrane of the ovum from which the villosities sprang was of cellular structure, and in the middle of the smooth part, turned towards the uterus, there was an opaque spot which might be taken for an embryonic area, and which presented internally a thin layer of finely granular nucleated cells. The ovum lay on the inside of the posterior surface of the uterus near the upper border, imbedded in the thickened mucous membrane or decidua, and having a thin covering of the same substance, which with the included ovum formed a rounded projection into the cavity of the uterus.

It may be doubtful how far the process of development had advanced

Fig. 664.

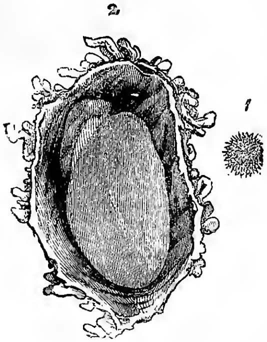


Fig. 665.

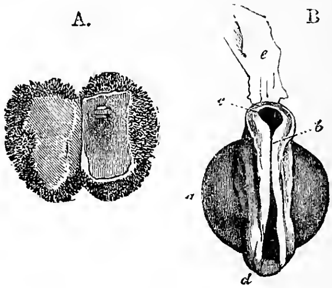


Fig. 664.—Human ovum of 12 to 13 days (from Allen Thomson).

1. The ovum of the natural size with simply villous chorion.
2. The same opened and magnified seven times. The large yolk-sac is seen with the embryo seen sidewise lying flat upon the yolk-sac.

Fig. 665.—Human ovum and Embryo of about 14 days (from Allen Thomson).

A. The ovum opened, half the chorion laid to one side and the embryo and yolk-sac seen in the other; natural size.

B. The embryo and yolk-sac viewed from the dorsal aspect, magnified about ten times; *a*, yolk-sac; *b*, hind brain portion; here for a space the medullary canal is closed; *c*, the mid-brain open superiorly; *d*, hinder part of the medullary canal also open; *e*, portion of membrane, perhaps belonging to the torn amnion.

in this ovum, but supposing Reichert to be correct in holding that no parts of the embryo had yet been formed, it would appear that in the human embryo villi may be developed from the blastoderm, as occurs in some animals, previous to the formation of a reflected amnion.

A somewhat similar case was observed by T. Wharton Jones (No. 118), in which also the side next the uterus was devoid of villi and there was no appearance of an embryo. Another instance observed by Breuss presented nearly the same phenomena. (No. 126).

The first appearance of the human embryo as a primitive trace, or with a simple medullary groove, has not been observed. Among the earliest human ova in which features of embryonic structure are distinctly recognisable are two first described by the writer of this section in 1839 (No. 119), and another described by His (No. 132), which may have been even of a slightly earlier date.

In this stage the embryo, which consists almost entirely of its primary axial parts, lies prone on the surface of the yolk-sac, after the

manner of a chick on the second day or the rabbit on the tenth. The heart exists, and doubtless a vascular area on the surface of the yolk-sac, though not fully observed, was already the seat of the first circulation. From the researches of His it seems probable that in the two

Fig. 666.

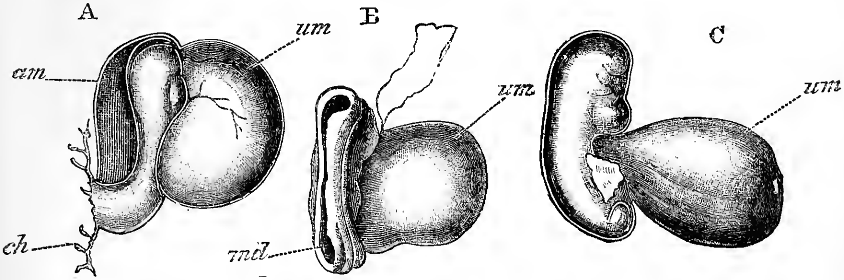


Fig. 666.—THREE EARLY HUMAN EMBRYOES (from Balfour after His).

A. An embryo of less than fourteen days, described by His. *am*, amnion ; *um*, umbilical vesicle ; *ch*, chorion to which the embryo is attached by a stalk.

B. Embryo of about fourteen days, described by Allen Thomson. *um*, umbilical vesicle ; *md*, medullary groove.

C. Embryo of sixteen or eighteen days, described by His. *um*, umbilical vesicle.

first mentioned specimens, the amnion, although imperfectly observed nevertheless already existed, but had been accidentally destroyed, and His is of opinion that in these and other similar cases the allantois, which in the human ovum is undoubtedly formed at a very early period, had

Fig. 667.

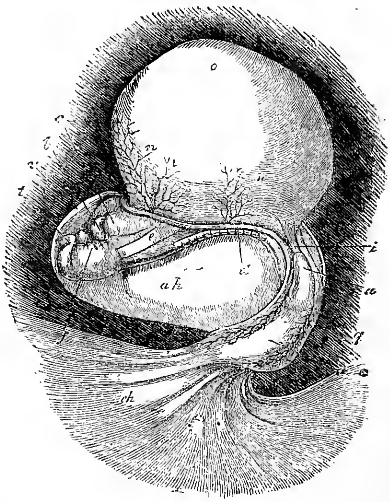


Fig. 667.—HUMAN EMBRYO OF 15—18 DAYS, WITH YOLK-SAC, AMNION AND UMBILICAL PEDICLE. Magnified (from Kölliker after Coste).

b, aortic bulb ; *c*, heart ; *d*, margin of the wide abdominal opening ; *e*, œsophagus ; *f*, branchial arches ; *i*, hind-gut ; *n*, *m*, vitelline vessels ; *o*, yolk-sac, its vessels not fully represented ; *u*, stalk of allantois ; *a*, allantois with distinct vessels forming a short umbilical cord united to chorion ; *v*, amnion ; *ah*, its cavity ; *ch*, chorion.

already grown out from the hinder part of the body of the embryo so as to become attached to the interior of the chorion, as illustrated by the accompanying diagram. (Fig. 670.)

Somewhat more advanced than the foregoing is the ovum well described by Coste (No. 22, iii.), which was probably of from fifteen to eighteen days, and of which the whole diameter was 13 mm., or fully half an inch. The embryo, of 4·4 mm. in length, lay upon a vitelline sack at one side of the cavity within the chorion, and was there fixed by an umbilical cord to the interior of that membrane, while a

distinct amnion enveloped its other side. The parts of the heart with the pericardium were distinctly recognisable, as well as several other points of structure belonging to the embryo, which will be referred to at a later period. The cephalic portion of the intestine was formed and enclosed, but the larger hinder part was no more than a groove opening widely into the yolk-sac (fig. 667). The vitelline vessels were distinct on this last. The chorion was uniformly covered with villi, which were hollow; and the vascular layer of the allantois ran inside it without however yet penetrating the villi.

An embryo described by His, marked L in his Monograph, presents some of the same features. (Fig. 666, A.)

In human ova which may be estimated as approaching the term of three weeks after conception, the body of the embryo is found to be curved, the cephalic flexure has also taken place, several of the pharyngeal bars and clefts appear below the cranium, and the communication between the intestine and yolk-sac is much reduced in size, though still wide.

Fig. 668.

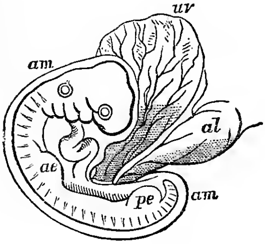


Fig 669.

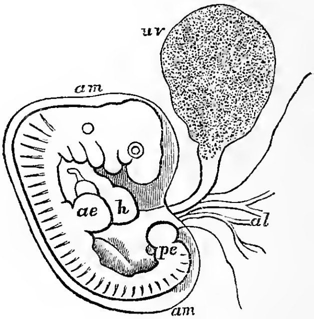


Fig. 668.—Outline of human embryo of about three weeks. $\frac{5}{1}$ (A.T.)

Fig. 669.—Outline of human embryo of about four weeks. $\frac{4}{1}$ (A.T.)

am, amnion; *uv*, yolk-sac; *al*, allantoid pedicle; *ae*, anterior extremity; *pe*, posterior extremity; *h*, heart.

In the next stage, of which the age may be reckoned as of fully three weeks (see fig. 668), the extremities begin to appear as semi-circular plates projecting from the lateral ridge of the body. The Wolffian bodies are formed, the visceral arches are now four in number, including that of the lower jaw, with the clefts between them, the intestine has become tubular and the vitello-intestinal communication is diminished in width. At four weeks (fig. 669) these features are more pronounced, the yolk-sac is pyriform, its duct is thin and elongated, and the extremities begin to divide into proximal and middle segments.

In the earliest stage at which the human embryo has been observed, or near the end of the second week, the symmetrical rudiments of the body lie prone upon the surface of the yolk-sac enclosed in an amnion and with an allantoid adhesion to the chorion. In the course of the third week, the midgut becoming more and more tubular, the head and trunk of the embryo undergoing incurvation, and the abdominal walls converging ventrally, the umbilical aperture, which is at first very wide, contracts and embraces more closely the diminishing vitelline duct and the allantoid vessels; and by the sixth week the amnion, which was at first very close to the body of the embryo, is separated from it by

the increase of the amniotic fluid, and the umbilical attachment begins to elongate into a cord over which the amnion is inflected.

Up to this time the human embryo presents a remarkable resemblance to that of most mammals, and also to some extent of birds and reptiles of a corresponding stage of development; but in the period which follows, or from the sixth to the eighth and still more to the tenth weeks, the changes which it undergoes, though agreeing in their general nature with those which take place in other animals, are so modified as gradually to bring out the peculiar features which are characteristic of the human form and type of organisation. Among these the most marked are the large and early development of the cerebral hemispheres which gives peculiar prominence to the forehead and upper part of the head, together with the comparative small size of the maxillary and mandibular parts of the face, the form of the external auricle, and the form and attitude of the limbs.

Fig. 670.

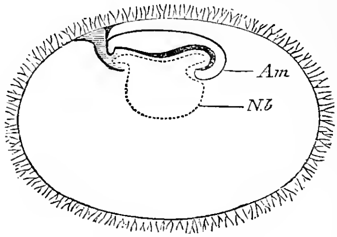


Fig. 670.—Diagrammatic section of the early human ovum according to His. (From Balfour after His).

Am, amnion ; *Nb*, umbilical vesicle.

It would have been desirable to give some account at this place of the rate of progress and the peculiarities of form and structure belonging to the successive stages of early growth and development in the human embryo; but the want of space and the paucity of materials for such an account as would be satisfactory forbid the attempt for the present, and oblige us to refer the reader to the useful plates of Erdl (No. 23), and to the important contribution to the subject made by His in the second part of his work on the human embryo (No. 132).

Returning to the subject of human uterogestation it is to be observed that the mode in which the connection of the embryo with the chorion is established by the allantoid pedicle and vessels, as well as the early condition of the amnion, present some peculiarities of which direct observations have not yet furnished a full explanation, or one which would bring the phenomena into conformity with the modes of development of the membranes hitherto most familiar to embryologists. But several recent observations seem to show that important deviations from the better known types of development among mammals may still be discovered by future investigations.

Fig. 671.

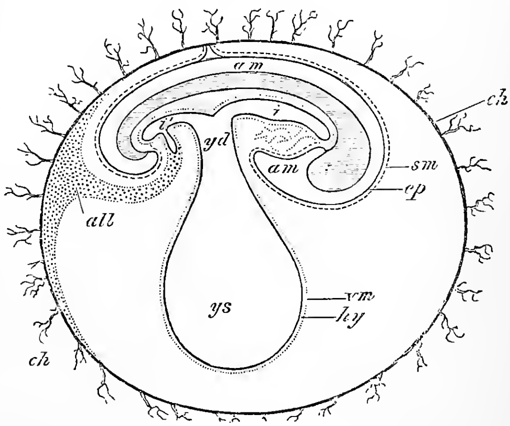


Fig. 671.—Diagrammatic outline of section of human ovum at three weeks (A. T.)

ch, chorion; *ep*, epiblast of reflected amnion; *sm*, parietal mesoblast; *am*, amnion; *ys*, yolk-sac; *all*, allantois; *vm*, visceral mesoblast (vascular layer); *hy*, hypoblast.

The view taken by His (No. 132, I.) that the outer layer of the human allantois is from a very early period in close proximity to, if not in actual union with the primitive chorion, would not be inconsistent with what is already known of the development of the membranes in most animals, if it could be supposed, as seems

necessary, that the mesoblast of the allantois extends itself in the intermesoblastic space, and is therefore at first within a caudal or equivalent fold of the amnion. It is difficult indeed to conceive how the vascular layer of the allantois could pass round the whole interior of the chorion, except in a space formed between the outer and inner folds of the amnion.

Schäfer's observations in the guinea pig (No. 100, ii.) and Fraser's in the Rodentia, sufficiently show how early the vascular layer of the allantois may extend itself towards the chorion in some tribes of animals, and the researches of His on early human ova, as well as those of Coste and others go far to prove the early union in a peculiar manner of the outer layer of this membrane with the chorion.

2. **Enclosure of the Ovum in the Uterine Decidua.**—It is now well known that the uterus is prepared for the advent of the ovum by the increased development of certain parts of its mucous membrane which give rise to the decidua.

A similar change takes place previous to every menstrual period, but in case of pregnancy occurring there is no exfoliation of the membrane such as follows in menstruation, but on the contrary the development of the decidual elements of the mucous membrane progresses to a much greater degree. These changes are probably of two kinds, the first consisting mainly in the increase of the subepithelial cellular elements of the mucous membrane, together with a dilatation and subsequent atrophy of parts of the utricular glands, and the other in a great enlargement and change of structure of the uterine blood-vessels, which together prepare the way for the formation of the maternal part of the placenta in the more limited area occupied by that structure.

Embryologists were for long at a loss to understand how the human ovum, which enters the cavity of the uterus quite free from any reduplication of the uterine lining membrane, becomes very soon completely enclosed, or *incapsulated* in its substance. Nor have the actual steps of the incapsulation ever yet been directly observed. But the fuller knowledge of the nature of the change which the lining membrane of the uterus undergoes before and after the arrival of the ovum in its cavity, and the closer observation of the nature and relations of the material by which the ovum is enclosed make it extremely probable that, as was first suggested by Sharpey (No. 15, iii., p. 1580), the minute ovum, on entering the uterine cavity, and possibly being sunk in one of the depressions which lie between the bulging areas of hypertrophied mucous membrane, is gradually surrounded by a wall of the decidual substance, which rising from below encroaches more and more upon the surface of the ovum, and comes at last to cover it entirely and to exclude it from the uterine cavity.

When the ovum has been fully imbedded in the decidua, as at the third or fourth week, it forms along with the decidua a swelling or projection within the uterine cavity, on opening which the villous chorion is found everywhere surrounded by the substance of the decidua; but the part of the latter substance which passes over the free surface of the ovum, or that which is towards the uterine cavity, is thinner and simpler in its structure than at the place of attachment of the ovum and in other parts of the uterine surface; and its appearance at the most projecting part or summit, different from the rest, indicates, by a sort of cicatricial mark, the place where the substance of the decidua, as it gradually covered in the ovum, may be supposed to have finally closed.

The decidual thickening of the mucous membrane affects nearly equally the whole of the lining of the uterine cavity, but towards the os

internum, and across the fundus to the Fallopian tubes, the thickening, first suddenly and then gradually, decreases, and the membrane assumes the unaltered condition which is maintained in these passages.

By the changes now described there has become apparent the distinc-

Fig. 672.

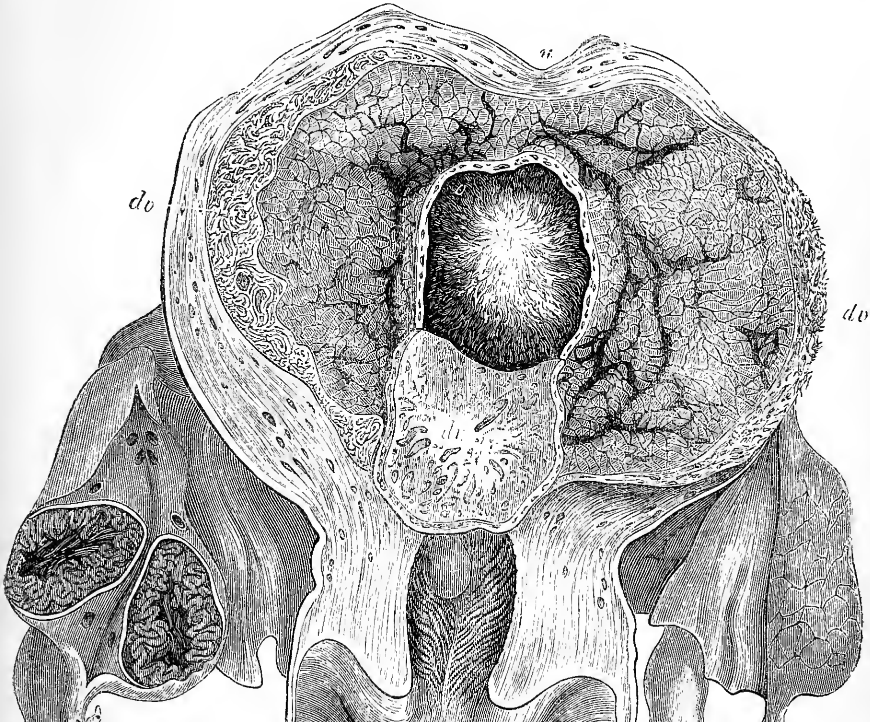


Fig. 672.—View of the interior of the human gravid uterus at the twenty-fifth day (from Farre after Coste).

u, uterine wall; *o*, villi of the chorion of the ovum; *dv*, decidua vera and enlarged uterine glands; *dr*, decidua reflexa, divided round the margin of the ovum, and turned down so as to expose its pitted surface, which has been removed from the ovum. The right ovary is divided, and shows in section the plicated condition of the early corpus luteum.

tion of the three portions of decidua usually recognised by authors, viz., *decidua vera, reflexa,* and *serotina.* The first of these is that portion of the altered membrane which lines the general cavity of the uterus in

every part except that occupied by the attachment of the ovum; the decidua reflexa is that which covers the ovum as it projects into the uterine cavity, and which is continuous with the decidua vera round the base of the swelling. The name of *decidua serotina* (or late formed) is most frequently employed to denote the layer or layers of decidual substance which intervene between the developed placenta and the uterine wall outside it; but by some it has been made to include also the part of this structure which originally enters into the formation of the maternal part of the placenta, thus including a placental and a uterine decidua serotina.

Fig. 673.

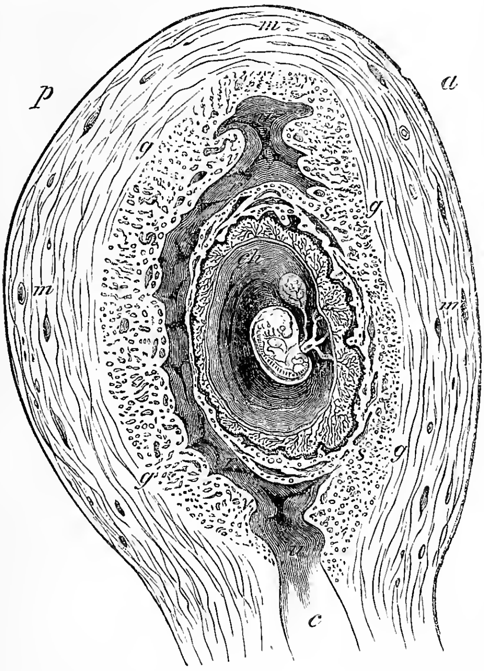


Fig. 673. — Semi-diagrammatic outline of an antero-posterior section of the gravid uterus and ovum of five weeks (A.T.).

This drawing is taken from a very perfect specimen of the uterus obtained from the body of a woman who died of cholera in 1849.

a, anterior uterine wall inside which was situated the placental attachment of the ovum; *p*, posterior uterine wall (the accessory parts being omitted); *m*, muscular substance of the wall; *v*, thickened lining membrane forming decidua vera, and showing grooves and eminences on its surface and enlarged glands and vessels in its substance; *g*, the glandular or deep layer; *r*, the decidua reflexa; *u*, indicates the uterine cavity; *s*, decidua serotina; *c*, cavity of the cervix uteri; *ch*, chorion with its villi, which are more highly developed on the placental side; *e*, the embryo enclosed in the amnion, with the allantoic vessels passing into the placenta, and the umbilical vesicle.

The blood-vessels and the glands of the mucous membrane also undergo great enlargement and modification. The whole of the decidua vera and the adjoining part of the reflexa are at first penetrated by blood-vessels derived from those of the uterus, more especially in the latter part of the second month, when the decidual structure may be considered as having reached its highest degree of development. After this time the blood-vessels of the decidua reflexa, and later those of the whole lining decidua of the uterus, except in the immediate vicinity of the placenta, shrink and ultimately disappear, so that the membrane formed by the united deciduæ becomes in the end wholly non-vascular. The same retrograde process, leading to atrophy and disappearance, occurs in the blood-vessels of the chorionic villi by which the decidua reflexa is penetrated, and, although the villi themselves never entirely disappear, but may be

traced even in the advanced stages of pregnancy as sparse and shrivelled irregular arborescent processes, the blood-vessels very soon begin to shrink and disappear from all the villi which do not form part of the placental structure. To the changes occurring in the decidua serotina as connected with the placenta reference will be made further on.

The Placenta.—The general relations of the fœtal and maternal structures of the human placenta are illustrated in an interesting manner

Fig. 674.

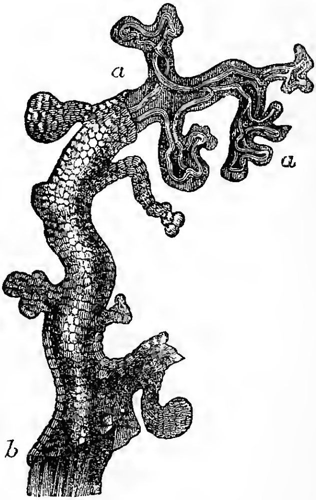


Fig. 674.—Chorionic villus from the placenta at the twelfth week. Enlarged 180 diameters (from Leishman after Ecker).

From *a* to *b*, the epithelial covering is left entire; from *a* to *a* it has been removed and the fibrous core with the capillary blood-vessels is shown.

by the study of the different forms which they present in various orders of mammals, or as it is called of their *placentation;* but limitation of space prevents our entering upon any full account of this subject, and the reader is referred to the works of Turner (No. 150, ii.), Ercolani (No. 147, iv.), and other authors.

The general result of recent researches on the Comparative Anatomy of the placenta may be thus stated. In all mammals, so far as is yet known, excepting the monotremata and marsupials, the true placental structures consist in the establishment of a close relation between finely ramified fœtal blood-vessels derived originally from the outer or mesoblastic layer of the allantois, with minutely or widely distributed blood-vessels belonging to the uterus. Both of these are originally at least, if not throughout the whole of gestation, accompanied and supported by cellular and other constituent elements of the fœtal and maternal structures to which the blood-vessels respectively belong; as, on the part of the fœtus, the villous ramifications of the chorion, and on the side of the mother a corresponding development of a part of the lining membrane of the uterus; while the uterine glands do not appear to take any direct or important part in this combination of fœtal and maternal elements.

a. Early Development of the Human Placenta.—The human placenta and that of the Apes are characterised, 1st, by the fact that the chorion derives its blood-vessels exclusively from the allantois, which are ramified in the villi to a very great extent and degree of minuteness, and, 2nd, by the enormous dilatation of the uterine vessels, and the very marked changes undergone by the decidual or perivascular tissue, which give rise to a structure different from that of any other animal.

All are now nearly agreed on general grounds that some combination of fœtal and maternal parts occurs in the formation of the placenta; but we are still far from having an exact knowledge of the manner in which the union is effected. Sufficient observations are in fact wanting to show in a series the successive conditions of the placenta during the period of most active change, *i.e.*, from the 5th or 6th week up to the

middle or end of the third month; and as the human placenta differs too widely from that of animals to admit of analogical reasoning, the views of authors who have offered explanations of the phenomena must, to a great extent, be regarded only in the light of more or less probable conjectures.

Numerous observations, however, would appear to make it extremely probable, if not actually a demonstrated fact, that an actual imbedding of a part or the whole of the fœtal villi in the substance of the decidua is a fundamental phenomenon in human placental formation (Schröder van der Kolk (No. 141), Langhans (No. 151, i. and ii.), Leopold (No. 156)), &c.

Fig. 675.

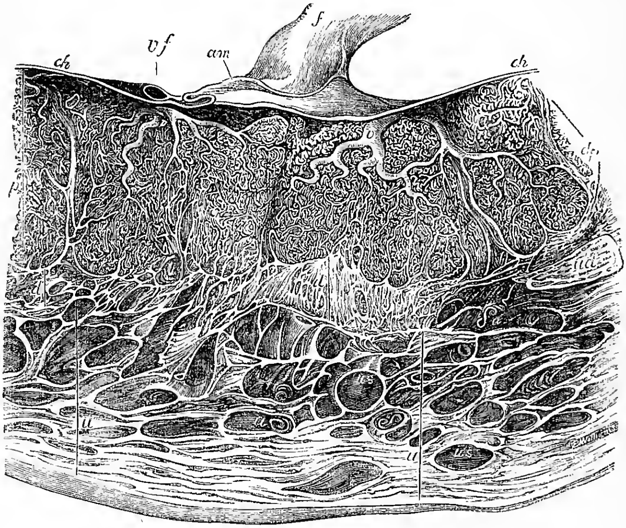


Fig. 675.—VERTICAL SECTION THROUGH THE MIDDLE PART OF THE PLACENTA AND THE UTERINE WALL (from Farre after Wagner).

The preparation was from a woman who died in the thirteenth week of gestation: the lines *u*, *u*, run through the wall of the uterus to the outer surface of the placenta; *d*, the decidua serotina; *p*, the tufts of fœtal vascular villi, of which two larger divisions are separated by decidual septa, as at *dp*; *f*, the placental end of the umbilical cord; *am*, the amnion; *ch*, the chorion; *vf*, divided fœtal blood-vessels; *v*, stems of vascular villi; *us*, uterine sinuses or veins; *a*, *a*, coiled arteries passing into the placenta.

The writer of this section thinks that he has obtained convincing proof of this imbedding in the specimen represented in fig. 673, as well as in others of a somewhat more advanced age (7 weeks); and, in the figure referred to, he has indicated the place and manner in which the imbedding of the villi may be supposed to occur by faint lines in the shaded space or interval represented between the tufts of villi and the firmer decidua in the region of the decidua serotina and the greater part of the reflexa.

Thus the villi become everywhere covered by or brought into close connection with delicate prolongations of altered decidual tissue, carrying with it loosely the much expanded uterine vessels reduced to the condition of gigantic capillaries.

But the main difficulty is to determine what afterwards becomes of

this decidual tissue, and what is the relation of the nascent condition of the placenta to its fully developed structure; and here, therefore, the principal divergence of opinion among authors arises; some holding, as Kölliker does, that the maternal elements, after having been combined with the villi in the manner before indicated, undergo atrophy and disappear so as to leave the fœtal villi provided only with their chorionic structures, and thus hanging naked into the maternal blood sinuses; and others, such as Ercolani, and in some measure also Turner, maintaining that a part of the maternal structure remains as a permanent covering of the villi, and that, after the acquisition of these new maternal elements, the original chorionic epithelium of the villi has disappeared in a greater or less degree. The writer is in the meantime most disposed to give the preference to the view advocated by Kölliker.

In this early process of development of the placenta it will be understood that the fœtal villi increase rapidly in their number, the complexity of their ramification, and the penetration of larger and smaller blood-vessels through all their branches. This development affects at first all the villi of the chorion except those near the most projecting part of the reflexa; but in the fourth and fifth weeks the increase in the number and bulk of the villi becomes much greater on the side next the uterus where the placenta is about to be formed.

In the decidua serotina, on the other hand, great differences have become apparent, among which is to be noted its division into two layers by large spaces which are probably dilated glands. The inner of these layers, which may be called placental, soon loses its glands entirely, and the other, the uterine or glandular, retains a considerable amount of glandular structure.

The maternal blood-vessels of the inner serotina, which at first had the ordinary characters of the arteries, veins, and capillaries of the lining membrane of the uterus, become completely altered by the atrophy and disappearance of the external and middle coats from the larger vessels, and by the conversion of them all into wide lacunæ or gigantic capillaries through which the maternal blood continues to flow. These lacunæ retain for a time their epithelial lining, but finally, when the interpenetration of the fœtal and maternal part is complete, the epithelium is lost to view, and is therefore either entirely absorbed, or, as supposed by some, remains as a delicate or homogeneous covering of the exterior of the villi.

In the early stages of placental growth the villi show frequent attachment to each other and to the decidual septa by means of processes which appear to consist of a degenerated granular form of the decidual tissue, and are probably the remains of the imbedding decidua.

The chorionic villi, in becoming imbedded in the decidua, lie first loosely in groups within honey-comb-like loculi hollowed out of the chorionic surface of the inner serotina. They undergo the further union and imbedding mainly by being overrun by the looser substance of the decidua, as supposed by the writer, and the walls of the loculi formed of the firmer decidua probably extend themselves in the form of the septa between the lobes.

In this part of the decidua the glands, which undergo a remarkable enlargement (see later) in the decidua vera, speedily disappear, and it is now well ascertained in animals, by the researches of Ercolani and Turner, that the fœtal villi do not, as was once supposed, penetrate into

the dilated cavities of the uterine glands, but are sunk in crypts of the decidua which lie between the glandular orifices. Nor is there any reason to believe that the villi enter the uterine glands in the formation of the human placenta. On the contrary, the observations of Schröder van der Kolk, Kölliker, Turner and others are quite opposed to such a view.

b. Structure of the Advanced Human Placenta.—After the middle of pregnancy, the placenta forms a large discoid or lenticular mass, of from four to five inches in its larger diameter and about three-quarters of an inch in thickness, interposed in a limited space between the fœtal membranes and the uterus. It presents a fœtal and a uterine surface, the

Fig. 676.

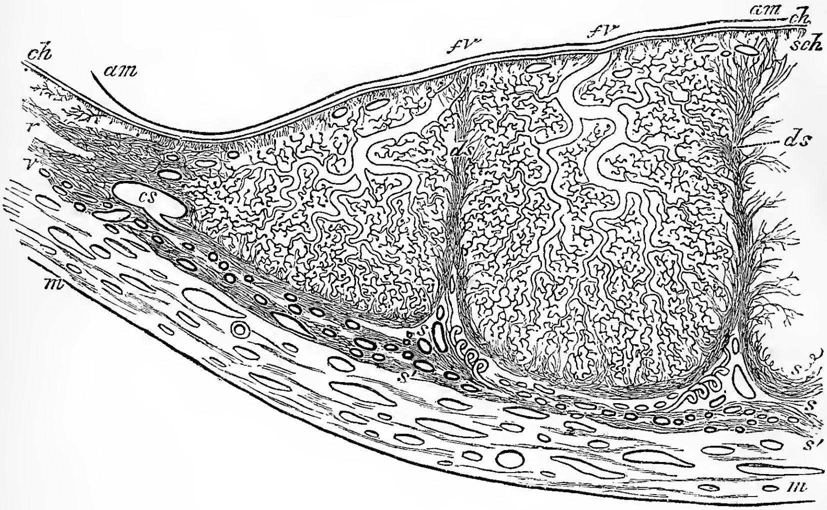


Fig. 676.—Diagrammatic representation of a section of the human placenta near the margin at five or six months (slightly enlarged). (A. T.)

am, amnion; *ch*, chorion; *fv*, stems of fœtal vessels passing into two of the placental lobes in the villi of which they undergo capillary ramification; *m*, muscular wall of the uterus with divided arteries and veins; *v*, decidua vera; *r*, d. reflexa; *s*, decidua serotina placentalis; *s'*, d. serotina uterina; *ds*, septa of decidua passing from the serotina between the lobes, branching into their interior, and reaching the chorion; in their bases are seen the maternal coiled arteries and the divided veins; *cs*, circular sinus; *sch*, the subchorionic decidual layer. An attempt is made in this diagram to show the union between the penetrating processes of reticulated decidua serotina and the villi of the lobes, the union extending in this, which is a marginal part of the placenta, as far as the subchorionic layer of the decidua.

former having implanted into it, usually near the middle, the umbilical cord, containing the allantoic or umbilical vessels, and covered by a tubular prolongation of the amnion. The placenta continues to increase in size with the fœtus, and when it has attained its full dimensions, it has a width of from seven to eight inches, or even more, and a thickness of about one inch and a quarter. Towards the circumference it rapidly thins, where it becomes continuous with the chorion and decidua. The fœtal surface is

covered by the chorion and amnion, and is traversed by the larger divisions of the umbilical vessels before they dip into the substance. The uterine surface shows a subdivision into a number of large lobes, sometimes called cotyledons, which are covered with a layer of decidua serotina passing over the whole of this surface, and sending septal prolongations into the placenta between the lobes, which may be traced in some places as far as the fœtal surface.

The more uniform parenchyma of the placenta within these lobes, which to the naked eye presents the appearance of a minutely divided sponge, consists in greatest part of highly-developed and complicated tufts of fœtal villi which adhere to the chorion by vascular stems of considerable size and strength, and subdivide again and again into minute and complex ramifications. Between the innumerable subdivisions of these tufts are the irregular vascular spaces or lacunæ, the outlines of which follow closely the ramifications of the villi throughout every inflection of their surface. These spaces, which are filled with the maternal blood and are continuous with the uterine vessels, are doubtless to be regarded as belonging to the maternal system, but their minute structure and anatomical relations have been so greatly modified in the progress of the placental growth, that, as already stated, it has been found very difficult to determine their exact nature in the fully formed condition.

On its outer side the placenta is united to the uterine wall by the decidua serotina, consisting, as already mentioned, of two layers, of which the inner alone enters directly into the formation of the placenta. From this inner layer of the serotina septa are prolonged between and surround more or less completely the lobes, so as to separate them from one another with very obvious but interrupted bands of decidual tissue; and from these interlobular septa irregular branched processes run into the interior of the lobes and through the placenta, so as even to reach the chorion in many places, and to unite with the subchorionic layer of decidua which extends from the margin of the placenta upon the chorion for a considerable distance, if not over its whole placental surface; and it thus becomes apparent that both fœtal and maternal (or decidual) structures are intimately intermixed throughout the whole thickness of the placenta.

A minuter examination of the spongy or finely divided portions of the placental lobes shows that in these the innumerable terminal villi of the branched fœtal placental tufts lie or hang for the most part free in irregular spaces (intervillous lacunæ) filled with the maternal blood; but they are not entirely loose, for, beside the stalks on which they are set, in numerous places they are attached at their tips and also on their sides by slender bands and sometimes finer filaments of very irregular form and of a granular fibro-nuclear substance, which pass from one to another of the villi, and between them and the processes of the decidua serotina, and which seem to be composed of decidual elements; forming thus according to Turner a network of trabeculæ derived from the decidua serotina in the interspaces of which the villi are contained (150, iii.).

The maternal blood spaces present the most varied and irregular forms, which scarcely admit of description, and, as they all intercommunicate freely, may rather be compared to a labyrinth, the walls of which are entirely formed by the villi over which they are moulded; so

that it is obvious that the villi, with whatever covering they may possess, are in full contact with the maternal blood which permeates all the intervillous spaces or lacunæ.

The fœtal villi present from a very early period, and long before they have entered into any combination with the uterine structures, a distinct external covering of epithelium which may be called chorionic, and as soon as they become vascular their interior is occupied by a core of connective tissue in which the fine divisions of the allantoic vessels are imbedded. In the more advanced stages of placental growth an increase of the fœtal vessels corresponding with the prodigious ramification and extension of the villi takes place, and besides the deeper loops of capillary and other vessels which occupy the interior of the villi there is developed also a more superficial capillary network (Schröder van der Kolk, No. 141); but in other respects the individual or terminal villi do not appear on a superficial inspection to differ greatly from those of the earlier stages.

On the other hand, there is good reason for regarding the maternal blood-spaces of the advanced placenta as essentially enlarged and altered decidual blood-vessels; for though the whole steps of the process of conversion have not been traced with sufficient fulness or accuracy, we are not without evidence from observation (Virchow, No. 142, and Priestley, No. 144) that the intervillous lacunæ must owe their origin to the disappearance of the decidual arteries and veins as such and the enormous dilatation of their capillaries around the villi, and to the thinning away of the decidual tissue in which they were previously distributed.

Microscopic observation has shown that the peculiar coiled vessels which pass through the serotina as the prolongations of the uterine arteries are destitute of the middle and outer arterial coats, but are lined with epithelium, and open directly by sudden enlargement, and without the intervention of any capillary vessels, into the wide cavities of the placental sinuses, and further that these sinuses are brought into direct communication with the larger uterine veins by means of considerable venous canals, lined with epithelium, which pass in a slanting manner through the decidua serotina, as well as by others which join the venous plexus named the circular sinus situated round the margin of the placenta.

Relation of the Fœtal and Maternal Elements in the fully-developed Placenta.—Such being the history of the fœtal vessels, and the maternal blood-spaces in the placenta, there still remain the important and difficult questions which have been long discussed, and which have not yet received a satisfactory solution—viz., What has become of the decidual tissue, and the maternal vascular lining in the developed placenta? Have they been entirely removed by atrophy and absorption, or are they still persistent, and are their remains still to be found as coverings of the villi, or in any other form?

As holding the first of these views Virchow, Kölliker, and Leopold may be quoted; and as supporters of the second, Schröder van der Kolk, Ercolani, and Turner.

It would occupy too much space to attempt any review of the arguments adduced in favour of these opposite views; and we must therefore refer the reader to the works of the authors quoted in connection with this subject, remarking at the same time, that while the greatest share of probability seems on general grounds to belong to the first view, or that of Kölliker, viz., that the villi retain their original epithelium, and that the maternal structure must have suffered atrophy and disappearance; the other opinion is not without some evidence in its favour. And more especially if it could be shown, as Ercolani

asserts—and in this he is supported by Romiti (No. 157)—that in the villi of the tenth week both the fœtal and maternal epithelium are still present together, while the fœtal or deeper epithelium appears to be undergoing atrophy preparatory to its removal, the view taken by that author, that in the formation of the placenta the decidual cells are substituted for the fœtal epithelial covering, and possibly also that a thin layer, representing the lining epithelium of the maternal vessels, overlays it externally on the surface of the villi, might receive important confirmation.

But, as before remarked, further researches are still required in the period of placental development, extending from the fifth or sixth week onwards into the third and fourth months, to enable us to determine the precise manner in which the peculiar condition of the maternal sinuses in the human species and in Simiæ is brought about. There can be little doubt that this condition is essentially different from that which has been well shown by the researches of Turner and Ercolani to prevail in other animals, in which it appears that, along with the fœtal capillary blood-vessels, and the epithelium of the villi, there are always present distinct maternal elements, in the form of capillary or other vessels lined with epithelium, and a certain amount of obvious decidual tissue surrounding them.

Relation of the Uterine Glands to the Placenta.—It has already been stated that the villi do not penetrate into the uterine glands of the human placenta. These glands undergo, it is true, in the earlier three months of uterogestation great enlargement and modification of their form. In the decidua vera especially the enlarged state of the glands is well known and very apparent in the early months of pregnancy; but as the membrane thins out in the later months, they are much flattened and atrophied, but are not entirely lost. In the inner layer of the decidua serotina they very soon become obliterated and disappear, but in the outer or uterine layer their cavities remain in a much widened condition, though drawn out and flattened; and it seems as if they gave rise in part to the separation of the outer and inner layers, where the severance afterwards occurs in parturition. In the outer layer, however, the glands are preserved in such a state as to be capable of restoration after parturition in that part of the mucous membrane.

The outer layer of the serotina is also the principal seat of the development in the latter half of pregnancy of the largest or giant multinuclear cells, which are characteristic of that layer in man, as well as in many animals. In connection with these cells, it is proper to mention the important discovery made by Friedländer (No. 152), and confirmed by Leopold (No. 156), according to which it appears that the main veins of the serotina and the adjacent part of the uterine wall undergo in the later stage of pregnancy a process of gradual obliteration by the ingrowth of the giant cells into the interior of the veins—a process which begins in the eighth month, and goes on progressively up to the end of gestation, and which seems to have the effect of producing stagnation and stoppage of the passage of the blood through the veins, and may probably be a factor in the induction of the act of parturition.

Placental Circulation.—The existence of a distinct circulation of blood in the fœtal and in the maternal vessels of the placenta, discovered by the Hunters, has long been placed beyond doubt by the experimental investigations of all those who have injected the two sets of vessels with sufficient care and success. By artificial injections fluids can be made to pass from the umbilical arteries through the capillaries of the villi into the veins, or in the reverse direction from the veins into the arteries. Nor does there ever occur, except from ascertained accidental rupture of the vessels, either extravasation of the injected material into the intervening tissue, nor any escape into the maternal sinuses.

The result of artificial injection of the blood-vessels in the pregnant uterus equally demonstrates the nature of the circulation in the maternal part of the placenta, for it is easy to show by this method that a fluid thrown into the uterine arteries passes through the coiled vessels and fills all the maternal blood-spaces of the placenta, surrounding everywhere the chorionic or fœtal villi, and returns thence into the uterine veins by the slanting venous channels, the *utero-placental sinuses*, lined with epithelium, which issue from the placenta at its uterine surface by piercing the decidua serotina, and which are also very

numerous towards the circumference of the organ, where they are in communication with the venous plexus or so-called circular sinus. Some of these veins may even be traced for some distance into the placenta, in the septa of decidual substance, which are prolonged from the decidua serotina between the lobes. (See Turner, Kölliker, and others).

Separation at Birth and Restoration of the Uterine Membrane.—In the act of birth a large part of the decidual structures which have been formed in human uterogestation, including that which is strictly placental, the whole of what remains of the d. reflexa and a considerable part of the d. vera, now fused into one thin covering of the chorion, are separated from the uterus, together with the fœtal placenta, the membranes, and all that belongs to the ovum. Thus in parturition, by the effect of uterine contraction, the fœtus is first expelled; the detached placenta follows, and carries with it the inner layer of serotina, the coiled arteries and the slanting veins being broken through; next come the inverted membranes of the ovum, together with the remains of decidua reflexa and part of the vera, which are finally peeled off the whole of the interior of the uterus. On the uterine surface a part of the decidua vera remains, and also the uterine decidua serotina lying next the muscular wall of the uterus. In this layer are imbedded the remains of the convoluted uterine glands, which extend outwards into the substance of the muscularis mucosæ. These are soon prolonged to the uterine cavity, a ciliated epithelial lining is formed on the inner surface, and the natural structure of the whole membrane is thus completely restored.

II. DEVELOPMENT OF THE SYSTEMS AND ORGANS OF THE EMBRYO.

It will be convenient to treat of this, which is the most extensive division of our subject, under the following sections, viz.:—1. The External Form and Framework of the Body; 2. The Nervous System; 3. The Vascular System; 4. The Alimentary Canal and Associated Organs; 5. The Urinary and Generative Organs.

I. EXTERNAL FRAMEWORK AND WALLS OF THE BODY; THE SKELETON, VOLUNTARY MUSCLES AND INTEGUMENTS.

In the most general morphological view of the development of the external frame-work of the body, its parts may be regarded as being moulded in certain definite relations according to the vertebrate type upon the cerebro-spinal nervous centre and its containing cranio-vertebral cavity, and in their commencement they present the form of body-segments or somites, which in the trunk correspond in number with the vertebræ, but in the head follow a somewhat different arrangement. It will be convenient to begin with a short statement of the earliest phenomena of the development of the embryonic axis.

I. FIRST RUDIMENTS OF THE EMBRYO.

These consist mainly of four parts which, named in the order of their commencement, are the primitive streak, the medullary canal, the notochord, and the protovertebral somites. The first of these is essentially a temporary and evanescent structure; the third, round which the column of vertebral bodies is formed, though also transitory, is somewhat more persistent than the first; the second and fourth, as the foundation of important organs, may be regarded as permanent.

1. **The Primitive Streak or Trace.**—The earliest indication of the formation of the embryo is in the *primitive streak* which appears about the twelfth hour of incubation in the chick, and on the seventh day in the ovum of the rabbit, in that part of the embryonic area which, with

Fig. 677.

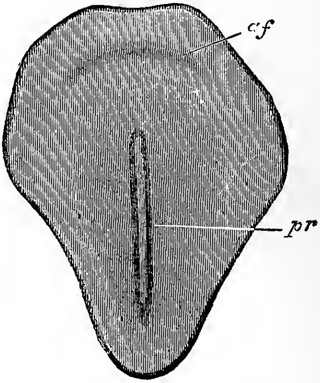


Fig. 677.—Pyriform transparent area of the chick's blastoderm with the primitive groove.

pr, primitive streak and groove; *af*, amniotic fold commencing; the darker shading round the primitive streak indicates the extension of the mesoblast.

reference to the position of the embryo, may be called the hinder, and which also is the narrower part when the area has become pyriform. It has not at first a linear or elongated form, but begins as a comparatively short sickle-like thickening of the blastoderm at the margin of the embryonic area, and subsequently stretches inwards upon the area, in the form of a narrow strap-like opacity, as previously described at p. 748. It is closely connected with the epiblast or upper layer, and its formation seems to consist more immediately in a proliferation of cells from the lower surface of that layer which results in the development of the mesoblast or middle layer through the whole length of the primitive streak, in which the epiblast and mesoblast are thus rendered continuous.

Fig. 678.

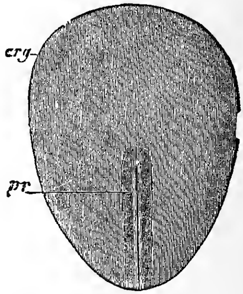


Fig. 678.—Embryonic area from the ovum of a rabbit of eight days. $\frac{22}{1}$ (From Kölliker.)

arg, border of the embryonic area; *pr*, primitive streak with groove.

In the course of its formation the primitive streak acquires a groove, the *primitive groove*, which arises from a depression in the epiblast at its upper surface. This groove does not usually extend to either end of the streak, but presents near its anterior extremity most frequently, but elsewhere also and somewhat variably in birds one or more depressions which are found to run through the blastoderm and indicate an interesting relation of the streak to the blastopore and neurenteric communication previously referred to (p. 759). The hypoblast takes no share in the production of the primitive streak, but runs across the area free and flat beneath it.

The primitive streak and groove were at one time confounded with the commencement of the true cerebro-spinal axis; but it was shown by the observations of Dursy in 1867 (No. 90), and has been fully proved by His (No. 29, i.) and others following him, that it does not give rise to any part of the nervous centre nor to any other important organ,

but on the contrary, is in a great measure transitory and evanescent in its nature; for though at first it indicates truly the direction of the embryonic axis, we shall find that it is thrust more and more backwards by the medullary and vertebral rudiments as they progressively grow in front of it, and it seems at last to be lost in the tissue below the caudal

Fig. 679.

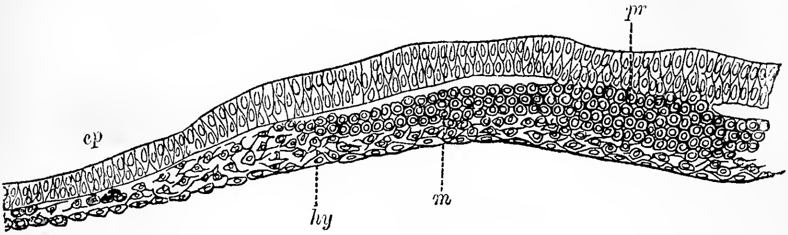


Fig. 679.—TRANSVERSE SECTION THROUGH THE FRONT END OF THE PRIMITIVE STREAK OF THE CHICK OF ABOUT 12 HOURS. (From Balfour.)

pr, primitive groove; *m*, mesoblast; *ep*, epiblast; *hy*, hypoblast.

extremity of the embryo. Its real significance therefore lies mainly in its relation to the origin and connection of the layers of the blastoderm and their apparent invagination at a period preceding the first development of the cerebro-spinal nervous axis of the embryo.

Fig. 680.

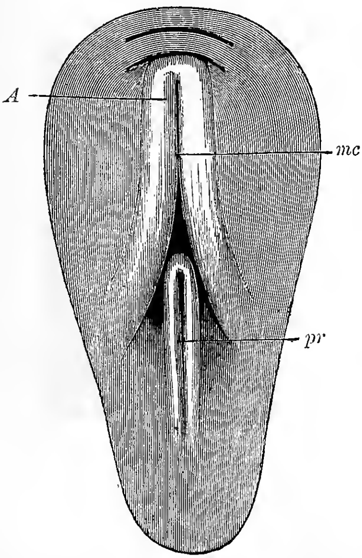


Fig. 680.—SURFACE VIEW OF THE TRANSPARENT AREA OF A BLASTODERM OF 18 HOURS, SOMEWHAT DIAGRAMMATIC. (From Balfour.)

pr, primitive groove, closed in front by the coalescence of the two lateral ridges; *mc*, medullary groove, having on each side the medullary folds or ridges, A, which also meet in front to enclose the groove, but diverge behind so as to enclose the primitive streak; in front the fold of the amnion is commencing.

2. **Medullary or Neural Centre.**—The first rudiment of the great neural centre makes its appearance somewhat later than the primitive streak, viz., in the chick about the eighteenth hour, and in the rabbit's ovum on the seventh day. It takes place entirely within the epiblast or outer layer, and depends on the growth of the cells of that layer in the anterior part of the embryonic area where it extends in the same direction as the primitive streak so as to occupy that part of the area left vacant by the latter.

The medullary plates which result from the thickening of the epiblast are at first comparatively short, corresponding mainly to that which will ultimately become the cephalic part of the nervous centre. They soon,

Fig. 681.

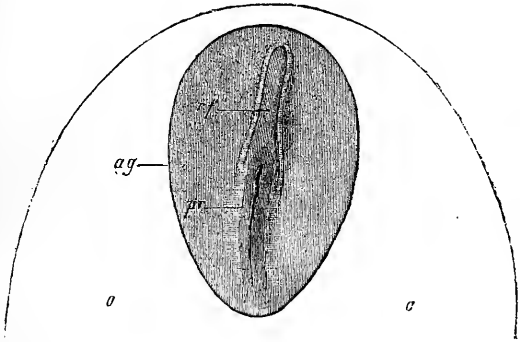


Fig. 681.—EMBRYONIC AREA, WITH OUTLINE OF THE VASCULAR AREA, FROM A RABBIT'S OVUM OF SEVEN DAYS. $\frac{28}{1}$ (From Kölliker.)

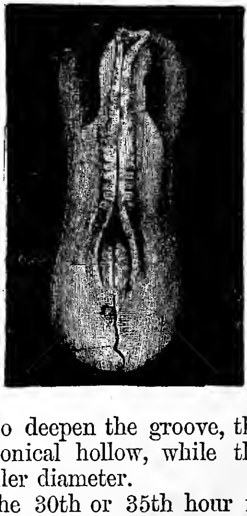
oo, vascular area; *ag*, embryonic area; *pr*, primitive streak and groove; *rf*, medullary groove.

however, elongate, and increasing in their thickness at the outer margins, they rise into lateral ridges, which are separated by a groove or furrow, while they run into one another, or are joined together round the cephalic extremity of the groove. Behind they diverge somewhat, and

Fig. 682.—DORSAL VIEW OF A BLASTODERM AND EMBRYO CHICK HAVING FIVE MESOBLASTIC SOMITES. (From Balfour.)

a.pr, anterior part of the primitive streak; *p.pr*, posterior part; the medullary ridges have come together in the greater part of their extent, but have not yet united; the caudal swellings are visible on each side of *a.pr*.

Fig. 682.



there they extend for some distance on either side of the primitive streak, so as to enclose nearly its anterior half between them.

As the formation of the medullary plates and groove progresses, they extend more and more backwards, so that the addition of new substance in the primitive or axial embryo takes place mainly by interposition between the part already formed and the primitive streak. As they extend backwards the ridges also rise more dorsally so as to deepen the groove, the cephalic part widens out into a somewhat conical hollow, while the spinal part remains of a more equable and smaller diameter.

In the next stage, which is completed by the 30th or 35th hour in the chick, and the 9th day in the rabbit, the medullary ridges of the epiblast bending round dorsally have met in the middle line above the medullary groove, and there coalesce, at first in a limited space near the

middle, and later both forwards and backwards, so as to effect the union along the whole dorsal line, except at the hinder incomplete part. By this union the medullary plates and groove are converted into the neural or medullary tube, which constitutes the primary form of the brain and spinal marrow.

Fig. 683.

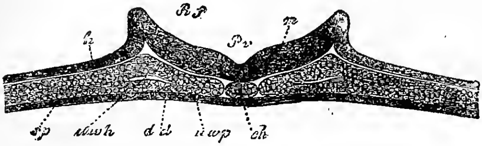


Fig. 683.—Transverse section through the embryo of the chick and blastoderm at the end of the first day. Magnified from 90 to 100 times. (From Kölliker.)

h, epiblast; *dd*, hypoblast; *sp*, mesoblast; *Pv*, medullary groove; *m*, medullary plates; *ch*, chorda dorsalis; *uwp*, proto-vertebral plate; *uwh*, commencement of division of mesoblast into its upper and lower laminæ; between *Rf* and *h* are the dorsal laminæ or ridges which by their approximation close in the medullary canal.

Fig. 684.

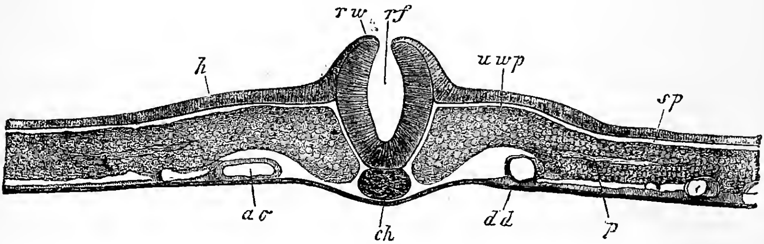


Fig. 684.—Transverse section of an embryo chick in the latter half of the second day, at the place where the vertebral somites cease. $\frac{83}{1}$ (From Kölliker.)

rw, dorsal ridges: *rf*, medullary groove or canal beginning to close; *uwp*, proto-vertebral plate; *sp*, lateral plate of the mesoblast; *h*, epiblast; *dd*, hypoblast; *ao*, primitive right aorta; *sp*, commencement of division of the mesoblast which forms the body cavity.

Fig. 685.

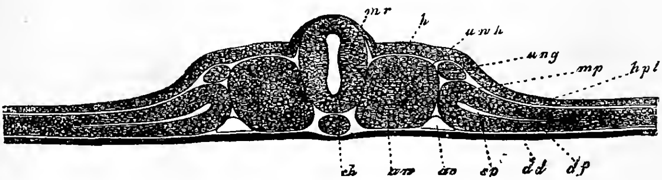


Fig. 685.—Transverse section through the embryo of the chick and blastoderm on the second day. (From Kölliker.)

dd, hypoblast; *ch*, chorda dorsalis; *uw*, primordial vertebræ; *mr*, medullary plates; *h*, corneous layer or epiblast; *uwh*, cavity of the primordial vertebral mass; *mp*, mesoblast dividing at *sp* into *hpl*, parietal, and *df*, visceral laminæ; *ung*, Wolffian duct beginning in the intermediate cell-mass.

3. **Notochord.**—The third rudiment of the embryo is the chorda dorsalis of von Baer or the notochord of more recent authors, which lies in the axis of the vertebral column and cranial base. When somewhat advanced, it extends through the forepart of the embryonic area from the

anterior extremity of the primitive streak to the front of the medullary canal; but, except at its hinder end, it has no immediate connection with the epiblast in which that canal is formed, and lies beneath it in the place which is afterwards occupied by the bodies of the vertebræ

Fig. 686.

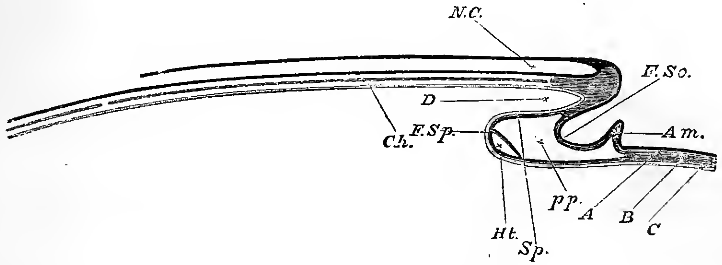


Fig. 686.—DIAGRAMMATIC LONGITUDINAL SECTION THROUGH THE AXIS OF AN EMBRYO-CHICK. (From Foster and Balfour.)

The section is supposed to be made at a time when the head-fold has commenced, but the tail-fold has not yet appeared. *A*, epiblast; *B*, mesoblast; *C*, hypoblast; *FSo*, fold of the somatopleure; *FSp*, fold of the splanchnopleure; *Am*, commencing (head) fold of the amnion: *NC*, neural canal, closed in front, but still open behind; *Ch*, notochord,—in front of it, uncleft mesoblast in the base of the cranium; *D*, the commencing foregut, or alimentary canal; *Ht*, heart; *pp*, pleuro-peritoneal cavity.

and base of the cranium. When fully formed it is also separate from the hypoblast which runs across below it. From this it might appear at first sight that it belongs to the mesoblast, by a part of which it is somewhat later surrounded. But there are still doubts with respect to its origin, that is, whether it is from the mesoblast or hypoblast. The former view is held by Kölliker, and for the higher vertebrates is in

Fig. 687.

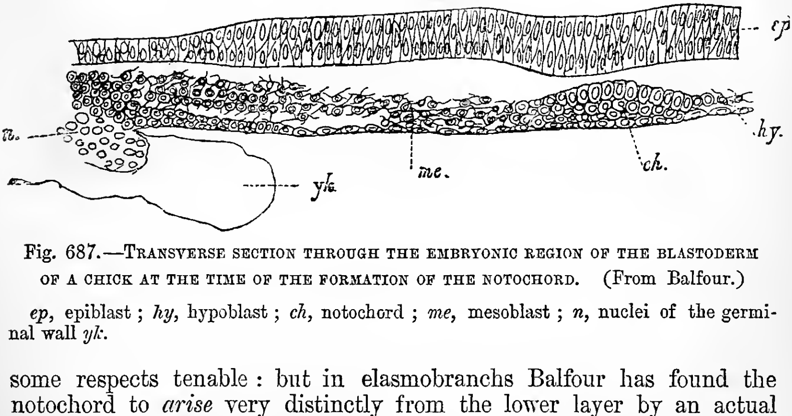


Fig. 687.—TRANSVERSE SECTION THROUGH THE EMBRYONIC REGION OF THE BLASTODERM OF A CHICK AT THE TIME OF THE FORMATION OF THE NOTOCHORD. (From Balfour.)

ep, epiblast; *hy*, hypoblast; *ch*, notochord; *me*, mesoblast; *n*, nuclei of the germinal wall *yk*.

some respects tenable: but in elasmobranchs Balfour has found the notochord to *arise* very distinctly from the lower layer by an actual infolding of a linear strip of the cells of that layer, and he, as well as some others, are disposed to attribute the origin of the notochord in the amniota to a similar source. With respect to this view,

it is to be observed that the hinder end of the notochord is directly continuous with the front part of the primitive streak where the mesoblast and epiblast are united, and if it does spring from the lower layer in front of that, it is still possible that in that situation the mesoblastic elements have not yet been differentiated from the hypoblastic in the primitive lower layer.

In the amniota the notochord is mainly cellular in structure; but in some of the lower vertebrates it becomes cartilaginous, and remains

Fig. 688.

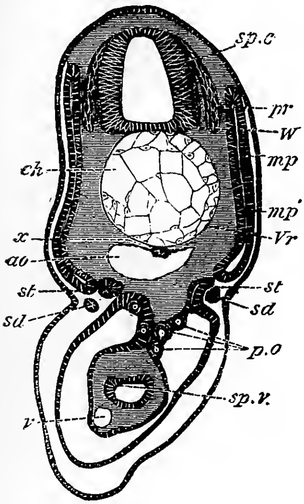


Fig. 688.—Section through the hinder part of the trunk of an embryo-shark, to shew the structure and relations of a large notochord. (From Balfour.)

spc, spinal canal; *ch*, notochord within its sheath; *ao*, aorta; *mp*, muscle plate; *vr*, rudiment of vertebral body. The figure is more fully described elsewhere.

as a permanent substitute for the true vertebral column. It is enclosed in a delicate, structureless, or cuticular sheath, outside which in the lower vertebrates, but not in the amniota, another sheath, viz., the elastic, is formed. It is upon the surface of the cuticular sheath in the amniota, and between it and the outer or elastic sheath in the lower vertebrates, that the mesoblastic substance derived from the inner part of the proto-vertebral column is deposited to form the matrix of the future vertebral bodies in a manner presently to be described. The notochord itself takes no direct part in the formation of the cartilaginous or osseous vertebræ; but its remains are to be found for a considerable time within the bodies of the vertebræ and intervertebral plates, as described by H. Müller (No. 159), and others in the human fœtus to a late period, and even in the child after birth.

4. **Mesoblastic or Protovertebral Somites.**—There is still another series of early developmental phenomena, which are nearly contemporaneous with the three previously referred to, and which, though not in themselves immediately concerned in the production of axial rudiments, are yet intimately associated with some of them, and have an important bearing upon the whole after-history of development. Soon after the appearance of the medullary plates and groove, and before the commencement of the closure of the medullary tube, there have appeared on each side of the dorsal ridges a row of well defined, dark, quadrilateral masses, situated in the adjacent column of mesoblast, and separated by clear transverse clefts, or linear intervals.

These masses were for long looked upon as the rudiments of the permanent vertebræ, and were called the *primordial* or *proto-vertebræ;* but they are now known to be of a more comprehensive nature, and receive the appellation of *mesoblastic* or *protovertebral somites.*

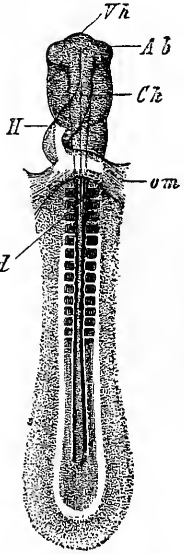
In now proceeding to explain the relation of these transversely divided segments to the other phenomena of development, we must

recall the fact, referred to in the account of development in general, that the great mass of the mesoblast is very soon divided longitudinally

Fig. 689.—Embryo-chick at the end of the second day, seen from below. $\frac{15}{1}$ (From Kölliker.)

Vh, forebrain ; *Ab*, primary ocular vesicles ; *Ch*, notochord ; *H*, tubular heart ; *om*, vitelline veins ; *Vd*, entrance to the forepart of the alimentary canal within the cephalic fold ; in the middle part of the embryo, the protovertebral somites are seen (to the number of thirteen pairs) on each side of the canal of the spinal marrow and notochord.

Fig. 689.



on each side into an inner thick column, in which the transverse segmentation into somites more immediately takes place, and which may be therefore named the *protovertebral columns*, and into flatter *lateral plates*, which again very soon become divided horizontally into an upper, or parietal, and a lower or visceral lamina, and have between them on each side the *body cavity*, or pleuroperitoneal space. At present we have mainly to do with the inner or protovertebral column.

The transverse cleavage of this column, giving rise to the protovertebral segments or somites, begins to appear very early at the side of the dorsal ridges, near the place where they embrace the primitive streak—a region which the subsequent condition shows to correspond with that of the anterior cervical vertebræ. But as the columns extend backwards, they

Fig. 690.

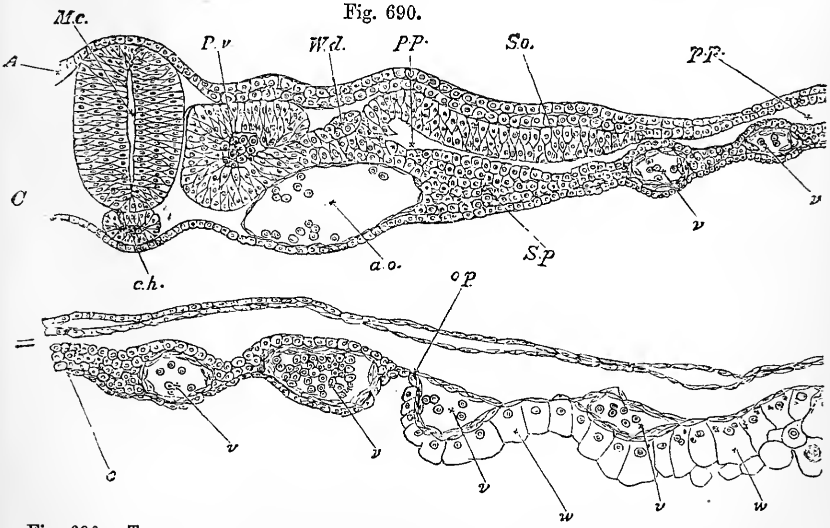


Fig. 690.—Transverse section through the dorsal region of an embryo chick of 45 hours. (From Balfour.)

A, epiblast ; *C*, hypoblast ; *Mc*, medullary canal ; *Pv*, protovertebra or mesoblastic somite ; *Wd*, Wolffian duct ; *So*, parietal mesoblast ; *Sp*, visceral mesoblast ; *pp*, pleuroperitoneal cavity ; *ao*, left primitive aorta ; *v*, blood-vessels ; *w*, germinal wall ; *ch*, notochord ; *op*, place of junction of transparent and opaque areas.

continue to undergo the transverse cleavage, so as to give rise to an increase in the number of the mesoblastic somites; and by the time when the medullary canal is closed, there are as many as ten or twelve of them. This process goes on progressively from the cervical into the dorsal, lumbar, sacral and caudal regions, till a number is attained, which corresponds closely with that of the permanent vertebræ, in which, however, the posterior or caudal segments are comparatively late in being formed.

The mesoblastic segmentation is at first confined to the inner or protovertebral column, and it is most distinct in that part; but in the later development of the walls of the trunk we shall see that a somewhat similar cleavage, or at least a differentiation corresponding with it, extends also into the parietal portion of the lateral mesoblastic plates, so as to give rise in them to the costal and intercostal divisions of the walls.

Fig. 691.

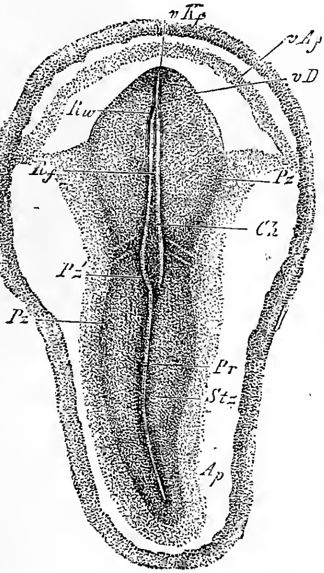


Fig. 691.—Area pellucida and rudiments of the embryo-chick of the second day. $\frac{19}{1}$ (From Kölliker.)

pr, primitive streak and groove; *Rw*, dorsal or medullary ridges meeting in front; *Rf*, medullary groove; *Stz*, axial zone; *Pz*, parietal zone; *Pz'*, two vertebral somites; *Ch*, notochord; *Vkf*, cephalic fold; *vD*, anterior intestinal fold shining through; *vAf*, anterior or amniotic fold; *Ap*, area pellucida.

The protovertebral column is at first solid, being composed of firmer columnar cells outside, and looser cellular elements internally. Soon, however, the somites become hollow by the liquefaction of the internal cells; and it is held that their cavity may be regarded as an extension of the general body cavity, or the intermesoblastic space, which is so apparent and constant in the lateral plates of the mesoblast (Balfour).

The mesoblastic somites by their further changes give rise to the main constituents of the body wall or framework, that is, the rudiments of the permanent vertebræ, and the muscular and dermal plates. These changes consist mainly at first in the separation of a mesial or internal part, in which the vertebral matrices are formed, from the outer parts which are converted into the muscular and dermal plates in a manner which will be more fully described under their respective heads.

II. FORMATION OF THE TRUNK.

1. **Vertebral Column.**—It is from the inner part of the protovertebral column before mentioned that the blastema of the permanent vertebræ is derived, the rapidly growing cells of which extending inwards and upwards from the protovertebral column, surround the whole of the chorda and the medullary canal with the first, or, as it has been called,

the membranous matrix of the vertebræ previous to their cartilaginous differentiation.

The part of this substance which surrounds the notochord forms at first a uniform or undivided tubular enclosure of the chord; but subsequently it shows transverse divisions corresponding to those of the protovertebral somites. The matrices of the arches, which are continuous with those out of which the bodies are formed, extend dorsally round the medullary canal and between it and the superficial epiblast, so as gradually to enclose the neural canal. These rudimental neural arches are from the first separate or in distinct strips, and thus intervals are left between them for the spinal ganglia and nerves which grow out from the nervous centre.

Fig. 692.

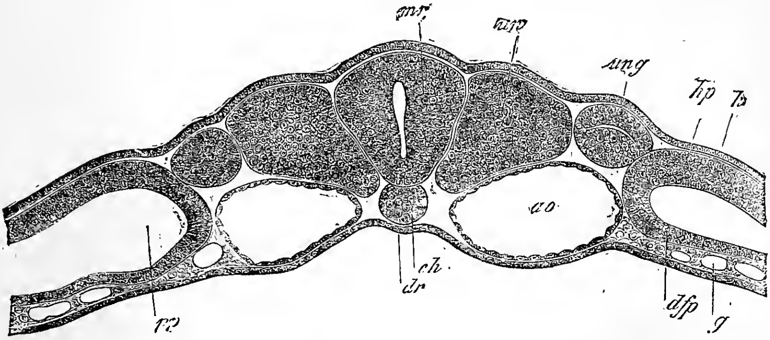


Fig. 692.—Transverse section of an embryo rabbit of 9 days and 2 hours in the middle dorsal region. $\frac{168}{1}$. (From Kölliker.)

mr, medullary tube; *uw*, protovertebral mass; *h*, epiblast; *hp*, parietal mesoblast; *dfp*, visceral division of the mesoblast; *pp*, pleuro-peritoneal cavity between them; *ung*, primitive segmental duct; *g*, vessels in the visceral mesoblast; *ch*, notochord; *dr*, intestinal groove of the hypoblast.

The next step in the formation of the permanent vertebræ is the chondrification or conversion into cartilage of the primitive or membranous matrix. This takes place nearly simultaneously in the bodies and arches, and is found on the fourth day in the chick, and the eleventh or twelfth day in the rabbit, and probably in the fourth and fifth weeks in the human embryo. In the process of chondrification the position of the divisions between the arches remains the same as in the original or protovertebral segmentation; but it is a remarkable fact, discovered by Remak (No. 25), that in the bodies the chondrification is accompanied by a change of such a nature that the separation of the permanent bodies comes to be effected by a new series of clefts, so situated between the former or protovertebral divisions as to cause the permanent intervertebral intervals of the bodies now to fall opposite to the neural arches and muscle plates, and the middle parts of the bodies consequently opposite to the place of the original protovertebral clefts.

While the chondrification of those parts of the vertebral matrices which are to form the bodies is proceeding, a differentiation of the blastema in the interspaces leads to the development of the fibrous substance of the intervertebral discs or ligamentous plates. And here

it is right to mention the changes of form in the notochord which are coincident with the formation of the parts surrounding it.

Fig. 693.

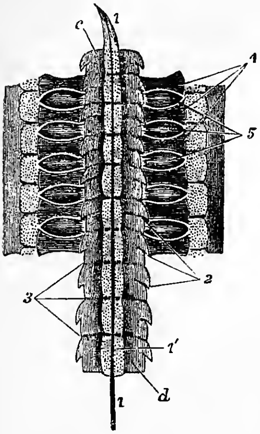


Fig. 693.—Cervical part of the primitive vertebral column and adjacent parts of an embryo chick of the sixth day, showing the division of the vertebral segments. (From Kölliker after Remak.)

1. 1, chorda dorsalis in its sheath, pointed at its upper end; 2, points by three lines to the original intervals of the primitive vertebræ; 3, in a similar manner indicates the places of new division into permanent bodies of vertebræ; *c*, indicates the body of the first cervical vertebra; in this and the next the primitive division has nearly disappeared, as also in the two lowest represented, viz., *d*, and the one above; in those intermediate the line of division is shown: 4, points in three places to the vertebral arches; and 5, similarly to three commencing ganglia of the spinal nerves: the dotted segments outside these parts are the muscular plates.

The notochord does not continue to grow as a whole in the same degree as the permanent vertebral parts, but on the contrary the greater part of it is in the higher vertebrate animals greatly reduced in proportional size, and constricted almost to a lineal filament in the most of its length. In each vertebral segment,

Fig. 694.

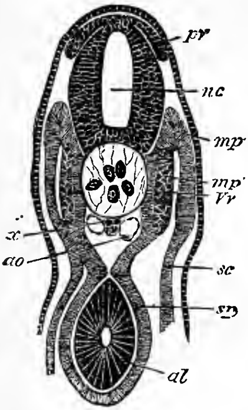


Fig. 694.—Transverse section of early embryo of pristiurus (elasmobranchs). (From Balfour.)

nc, neural canal; *pr*, posterior root of spinal nerve; *x*, subnotochordal rod; *ao*, aorta; *sc*, parietal mesoblast; *sp*, visceral mesoblast; *mp*, muscle-plate; *mp'*, portion of muscle-plate converted into muscle; *Vr*, portion of the vertebral plate which will give rise to the vertebral bodies; *al*, alimentary canal.

however, it presents dilatations or thickenings which differ somewhat in form and position in different animals according to the manner in which the permanent vertebræ are formed.

In mammals the constricted parts of the chorda are situated within the vertebræ, and the principal dilatations are in the intervertebral spaces, where they widen out considerably, and seem to form the basis of the pulpy or gelatinous substance which occupies the centre of the discs (Luschka, 1856, Kölliker).

In osseous fishes the dilatation is also intervertebral, and the growth of the chorda proceeds to such an extent as to give rise to the large double cone of soft and gelatinous substance which occupies the conical hollows of the biconcave vertebral bodies. But in birds, reptiles, and amphibia, the dilatations of the notochord are within the bodies of the vertebræ, and as in these animals articular cavities are developed between the vertebræ, the vestiges of the notochord very soon disappear from the intervertebral spaces, while they remain much longer visible in the bodies (Gegenbaur).

In mammals, therefore, the cartilaginous matrix of each vertebral body (and

the first subsequent ossification) begins in the centre immediately round the constricted part of the notochord: but it is also to be noted that within each

Fig. 695.

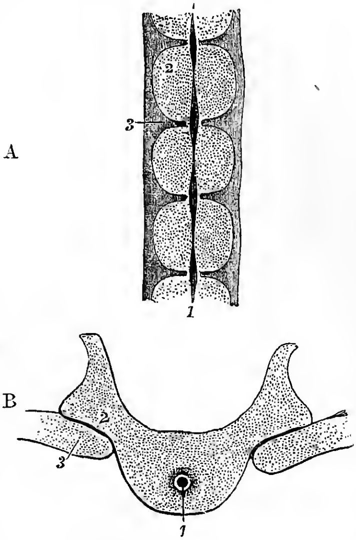


Fig. 695.—Sections of the vertebral column of a human fœtus of eight weeks. (From Kölliker.)

A, tranverse longitudinal section of several vertebræ. 1, 1, chorda dorsalis, its remains thicker opposite the intervertebral discs; 2, is placed on one of the bodies of the permanent vertebræ; 3, on one of the intervertebral discs.

B, transverse horizontal section through a part of one dorsal vertebra. 1, remains of the chorda dorsalis in the middle of the body; 2, arch of the vertebra; 3, head of a rib.

vertebra, at a somewhat later period, two small dilatations in the narrow part of the notochord are to be observed, opposite the intervals between the central ossifying nucleus and the epiphysial plates (see fig. 696).

In birds, reptiles, and amphibia, on the other hand, the formation of cartilage and the subsequent ossification of the vertebral bodies begin at the intervertebral surfaces, and extend from thence inwards upon their central part.

The neural arches of the vertebræ arise from a thin sheet of blastema which extends dorsally from the protovertebral columns on each side, and the two sheets, meeting each other mesially along the back (membrana reuniens superior of Remak), completely enclose the medullary

Fig. 696.

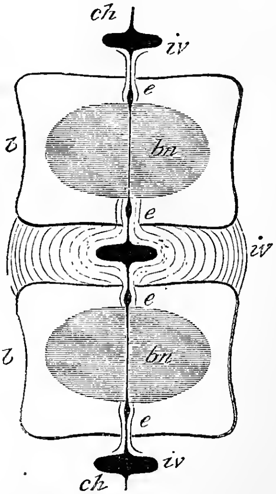


Fig. 696.—Diagram to show the position of the enlargements of the notochord in passing through the vertebral column. Half the natural size. (After Kölliker, A.T.)

ch, notochord; *b*, bodies of two vertebræ; *iv*, intervertebral plate with the wide enlargement of the notochord; *bn*, ossific nucleus of the bodies of the vertebræ; *e*, slight dilatations of the notochord opposite the epiphysial plates.

canal. This takes place on the third day in the chick, and is therefore considerably later than the investment of the notochord with the vertebral elements of the bodies.

The membranous investment of the medullary canal doubtless contains the elements not only of the neural vertebral arches, but also those of the dura mater and other coverings of the central nervous organs. This investment does not however form a complete tube, but is interrupted or open at the intervals occupied by the spinal ganglia and nerves emanating from the medullary centre. When chondrification of the vertebral matrices takes place the neural arches are found to be connected and at first continuous with the forepart of each vertebral body as reconstituted by the secondary transverse division, the intervals for the spinal nerves and ganglia being opposite the posterior part of the bodies and the intervertebral plates.

The history of the further development of the vertebral column belongs rather to that of the ossification of its several parts, which has been described in the first volume. It may be stated in addition here that in the human embryo the process of chondrification of the bodies begins between the fourth and fifth weeks (Kölliker), and is already completed by the sixth or seventh, soon after which ossification commences. In the arches the chondrification is about a week later in commencing, but the ossific deposit, which begins in the eighth week, is slightly earlier in them than in the bodies.

The whole number of cartilaginous vertebral matrices varies from 33 to 35, there being occasional subordinate variations in the number developed in each division of the trunk. The maximum number of coccygeal pieces is six according to E. Rosenberg (No. 166).

The formation of cartilaginous matrices for the vertebral arches begins first in those of the dorsal region, and extends from thence forwards into the cervical vertebræ and basis of the skull, and backwards into the lumbar and sacral vertebræ; but the dorsal extension of the cartilaginous matrix ceases to be formed in the hinder sacral and coccygeal vertebræ where these arches are afterwards deficient.

Rathke first showed (No. 14, ii., 1839) that the body of the Atlas vertebra is merged in the odontoid process of the second or axis vertebra; and that in the tortoise the chorda runs through the odonto-occipital ligament. This was confirmed for mammals by Joh. Müller, and later by Robin and Hasse. According to some the anterior arch of the atlas might belong to the subcentral or hæmal series of arches; but it would appear that the homology of this part is not yet fully determined.

2. **Ribs and Sternum.**—As completing the skeleton of the trunk of the body, it will be convenient to describe here the development of the ribs and sternum.

The ribs are extensions of the vertebral blastema in the thoracic parietal plate of the mesoblast; and their matrices are at first continuous with those of the vertebræ. They undergo early chondrification along with the vertebræ, but become separate from them before ossification commences. At their ventral extremities, as was first shown by Rathke in 1838 (No. 158), the seven which are afterwards to be sternal ribs of each side come to be united together by a longitudinal strip of cartilage; and the subsequent union of these two strips from before backwards gives rise to a single median piece of cartilage, which represents the manubrium and body of the sternum. The xiphoid cartilage is of later formation. (See Parker, No. 161.) This mode of origin and development of the sternum is interesting in connection with the malformation of fissure or median division of that bone which has been observed in many different gradations.

3. **Muscle Plates and Muscles.**—The muscles of the trunk derive their origin from the *muscle plates*, which are developed in the upper and outer part of the protovertebral column, in which the primary segmentation of the mesoblastic somites remains quite distinct. When the inner part of the protovertebral column has extended itself into the vertebral matrices of the bodies and arches (as before described), the muscle plates are found to consist of two laminæ, an inner and an outer, between which there is a space which is said to be in communication at first with the body cavity. This space is necessarily subdivided for each muscle plate. As development proceeds, however, the opening into the general body cavity being closed, the outer and inner layers of the plates lie more nearly applied together. The process of conversion into permanent muscular tissue by differentiation of the cells

has been shown by Balfour to begin first in the inner layer. (See fig. 694 and 698, *mp'*.)

The plates somewhat overlap one another; and connective tissue is deposited in the intervals between them, which in the lower animals is the basis of permanent intermuscular septa, and in the higher of temporary structures of the same kind, and of the perimysial sheaths, &c.

Fig. 697.

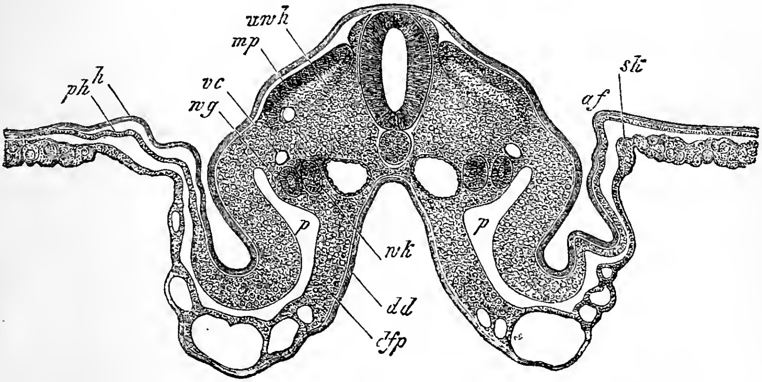


Fig. 697.—Transverse section through the middle of an embryo-chick of the third day, with open amnion. $\frac{40}{1}$. (From Kölliker.)

af, fold of the amnion consisting of *h*, epiblast, and *ph*, parietal mesoblast; *sk*, lateral fold of hypoblast and visceral mesoblast; *mp*, muscle-plate; *uwh*, remains of proto-vertebral cavity; *vc*, vena cardinalis; *wg*, segmental duct; *wk*, segmental tube; *p*, peritoneal cavity; *dfp*, visceral mesoblast with vessels; *dd*, hypoblast and intestinal groove.

In the progress of growth the muscle-plates extend to near the middle dorsal line; they reach also downwards in a ventral direction, and in

Fig. 698.

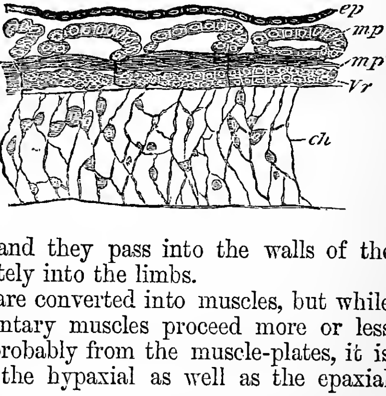


Fig. 698. — Horizontal section through the trunk of an early embryo of scyllium, passing through the notochord. (From Balfour.)

ch, notochord; *ep*, epiblast; *vr*, rudiment of vertebral body; *mp*, muscle-plate; *mp'*, portion of muscle-plate already converted into longitudinal muscles.

part under the vertebral bodies, and they pass into the walls of the body externally, and thence ultimately into the limbs.

Both layers of the muscle-plate are converted into muscles, but while it is undoubted that all the voluntary muscles proceed more or less directly from the mesoblast and probably from the muscle-plates, it is still questioned by some whether the hypaxial as well as the epaxial muscles proceed from this source alone.

In the early stages of muscular development in the amniota the myotomes are divided by transverse intermuscular septa, and thus retain much of the character

of protovertebral segmentation which is familiar as a marked feature of their structure in the lower vertebrates,—a fact of great morphological significance.

The formation of the longer muscles in the higher vertebrates takes place by the disappearance of the intermuscular septa and the longitudinal union of the fasciculi of successive myotomes. In the trunk the direction of these, especially of those most closely attached to the vertebral skeleton, remains for the most part longitudinal, but the more superficial muscles, and especially those connected with the limb-girdles, change their direction as well as their form to a great extent.

According to Balfour, the length of each muscular fibre derived from one of the cells of a muscle-plate is equal to the breadth of the myotome in which it is situated.

The division of the trunk muscles into an upper or dorso-lateral and a lower or ventro-lateral group by a horizontal septum, extending outwards from the transverse processes of the vertebræ and corresponding with that which belongs to the lateral line of the lower vertebrates, is only faintly indicated in the adult of the amniota.

4. **Body Walls.**—Along with the changes now mentioned as leading to the formation of the principal parts constituting the framework of the vertebrate body, there is to be noticed a later series of phenomena which are more immediately related to the production of the outer walls by which the visceral cavities and viscera are enclosed.

The parts hitherto described, which are mainly axial, lie prone and comparatively flat upon the surface of the yolk, and they are also chiefly formed by folding and differentiation of the two upper layers without any direct participation of the hypoblast, which passes thin and flat across the embryonic area below the medullary canal and notochord. But in the further progress of development, and in part simultaneously with the changes already described, the inflection of the peripheral parts of the blastoderm downwards or in a ventral direction, along with their extension and thickening, gives rise to the formation and enclosure of the thoracic, abdominal and pelvic cavities of the trunk.

The first of the folds now referred to, named the cephalic, begins to be formed much earlier than the rest, indeed its rudiment is to be perceived very soon after the appearance of the medullary plates and groove. It involves all the layers of the blastoderm, and is of such a nature as to pass downwards on each side, and gradually progressing backwards, to enclose a space within the layers which, as it is lined by the hypoblast, necessarily comprehends a part of the alimentary canal. This fold also encloses the rudiment of the heart when that organ comes to be formed, extending backwards below the cephalic part of the embryo as far as the fovea cardiaca, and closing in the cephalic part of the alimentary cavity anteriorly by the inflection of the three blastodermic layers below the primitive brain or cranium.

Somewhat later a similar inflection of all the layers occurs at the caudal extremity of the embryo, but this is much shorter than the cephalic fold, and includes therefore a comparatively small portion of the alimentary canal, viz., the caudal and primitive cloacal part, which, like the anterior, is at first completely closed by the inflection of the layers. (See fig. 660.)

Between the cephalic and caudal folds, that is, along the sides of the axial embryo in the greater part of what afterwards becomes the abdominal cavity, the walls of the body also undergo a downward inflection, and as these are continuous before and behind with the cephalic

and caudal folds, the place of their meeting, from being at first a wide and elongated gap between the cavity enclosed in the embryo and the peripheral parts of the blastoderm, becomes at last, by the gradual infolding of the edges bringing them more and more together, the narrower constriction which, from its later relations, is named Umbilical.

As, however, the infolding parts are everywhere composed of the parietal and visceral plates separated by the body cavity, we have to distinguish, in the umbilical constriction, the outer wall of the body formed of epiblast and parietal mesoblast, from the wall of the alimentary canal composed of visceral mesoblast and hypoblast.

Beyond the umbilical constriction the outer or parietal plate is in continuity with the amnion, and the deeper or visceral plate, when the intestine assumes a tubular form, is continuous with the yolk sac.

It thus appears, as was first shown by Von Baer, as the result of the earlier changes of vertebrate development, that there are formed two main tubular cavities, the one above the other below the notochordal axis; the upper being the cranio-vertebral, enclosing the great nervous centre, and the lower being the visceral cavity, in which the alimentary canal, heart, lungs and other nutritive organs are contained.

There is not at first any marked distinction between the head and the trunk in the axial part of the embryo, nor is there apparent any neck or cervical constriction. The changes which lead to this distinction are of later occurrence, and will be considered hereafter in connection with the description of the development of the head. Here it will suffice to state that the cephalic part of the axial body is at first only cranial, and that the face is formed later by the outgrowth of various bars and processes round the sense-capsules, mouth and pharynx, and mainly from the anterior and ventral aspects of the cranial part.

The caudal extremity of the embryo always consists of a prolongation of the vertebral column containing the notochord and covered by the usual epiblast. This extends beyond the place of the primitive caudal fold, and consequently the hinder part of the alimentary canal and organs connected with it fall short of the extremity of the tail.

The tail of the embryo is the seat of an incurvation which is most commonly ventral, but is sometimes combined with torsion, as is seen in a remarkable degree in serpents and in various degrees in other animals.

5. **Flexion and Torsion of the Embryo.**—Simultaneously with the occurrence of the early formative changes before adverted to, there take place others which affect the external form and attitude of the embryo. These consist mainly of three kinds of flexure and incurvation accompanied by various degrees of growth in the proportions of the parts in which they take place. The first may be named the

Fig. 699

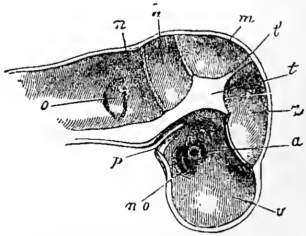


Fig. 699.—LONGITUDINAL SECTION THROUGH THE HEAD OF AN EMBRYO OF FOUR WEEKS. (From Kölliker.) $\frac{10}{1}$

v, anterior encephalic vesicle, cerebral portion; *z*, interbrain; *m*, midbrain; *h*, cerebellum; *n*, medulla oblongata; *no* and *a*, optic vesicle; *o*, auditory depression; *t*, centre of basi-cranial flexure; *t'*, lateral and hinder parts of tentorium; *p*, the fold of epiblast which forms the hypophysis cerebri.

principal cephalic flexure, and consists in a strong angular flexion of the cranial cavity in a ventral or downward direction in the region of the midbrain and sella turcica of the cranium. The second is, in birds, a more extended curvature of the vertebral column in the region of the neck and thorax, but in mammals more frequently in the lower cervical region only, such as to bend together the head and trunk of the body. The third inflexion is of a different nature from the first two, usually

Fig. 700.

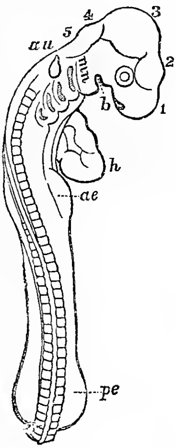


Fig. 700.—OUTLINE OF THE EMBRYO-CHICK AT THE END OF THE THIRD DAY, TO SHOW THE INFLECTIONS OF THE BODY AND THE COMMENCEMENT OF THE LIMBS. (After His.)

1 to 5 the cerebral vesicles; *h*, the mouth; *mn*, the lower jaw, and behind that the branchial bars and clefts; *au*, the auditory vesicle; *h*, the heart; *ae*, anterior extremity; *pe*, posterior extremity; the hinder part of the body is still prone upon the surface of the yolk, the head is now lying on its left side and between is seen the gradual torsion of the vertebral column and trunk.

preceding them in its commencement, and is more marked in birds and reptiles than in mammals; though it also occurs in some of the latter animals. This, as seen in birds, consists in a torsion of the embryo on its axis to the extent of a quarter of a circle, by which, beginning from the head, the embryo, from being at first flat and prone, comes gradually to have the left side lowest and applied to the blastoderm. In rare instances the direction of this torsion is reversed, and the embryo lies on its right side.

This torsion is not so constant in mammals as in birds, and it not unfrequently happens that along with the ventral incurvation of the body, the forepart, notched off from the rest of the blastoderm, sinks deeply into a hollow on the surface of the yolk.

There are, however, many differences in the early attitude of the embryo of mammals in connection with the varieties in the form and size of the yolk sac and other membranes.

III. ORIGIN AND FORMATION OF THE LIMBS.

The limbs arise as outgrowths from the lateral part of the trunk in determinate parts of the thoracic and pelvic regions, and, though not presenting any original protovertebral segmentation, are in some respects to be regarded as lateral extensions of vertebral somites in these situations. They make their first appearance after the completion of the primary steps in the development of the axial structures of the trunk, about the end of the third day in the chick (see fig. 700), and in the third and fourth week in the human embryo. They have the form of semilunar plates of parietal mesoblast covered with epiblast, budding out as it were from the lateral ridge, near the line of separation of the mesoblast into

its parietal and visceral laminæ, and close to the outer margins of the muscle-plates.

Each limb consists of the supporting arch or girdle, thoracic or pelvic, which is sunk in the substance of the lateral ridge, and makes little or no appearance externally, and of the free or projecting part which is at first quite simple, but soon becomes divided into the distal, middle and proximal segments.

Fig. 701.

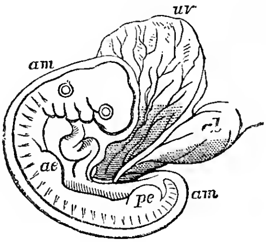


Fig. 701.—Lateral view of human embryo between three and four weeks, to show the commencing extremities. (A.T.)

am, the amnion surrounding the embryo; *uv*, umbilical vesicle; *al*, allantoid pedicle; *ae*, anterior extremity; *pe*, posterior extremity; the Wolffian ridge passing between them.

The lappet or bud which first shows itself appears to correspond most nearly with the distal segment comprising the hand or foot, the other two segments being successively developed between it and the root or girdle at an early period. The new part shows itself first by the notched separation of a segment between the terminal one and the side of the body, corresponding to the forearm or lower leg, and this is followed by the development in a similar manner of the proximal segment, the upper arm or thigh.

While these changes in the limbs occur, other advances in form and structure are discernible, first, in the appearance of four slight notches in the free margin of the distal segment, indicating the commencement of the pentadactylar division into the elements of fingers or toes, the formation of which is even more marked by the differentiation of the deeper substance of the distal segment; second, in the occurrence of an inflection between the middle and proximal segments, the hollow of which in the fore-limb looks forward, and in the hind limb backwards with reference to the axis of the trunk; and third, in the rapid progress of the deeper textural differentiation which leads to the development of the several components of the limbs, such as the skeletal, muscular, dermal, nervous and vascular parts.

Fig. 702.

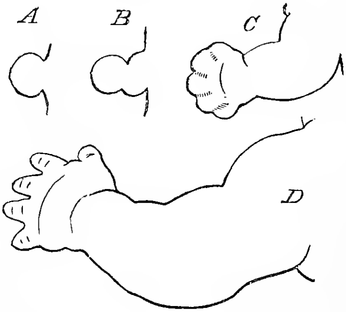


Fig. 702.—Outlines of the anterior extremities of human embryoes at different ages. (A.T., after His.)

A, at four weeks; *B*, at five weeks; *C*, at seven weeks; *D*, at nine or ten weeks.

The rudimentary limbs consist at first entirely of a mass of nearly

uniform blastemic cells derived from the parietal mesoblast, covered superficially by the cuticular epiblast, which always presents at its extremity a peculiar pointed or conical cap of thickened epidermis. (See fig. 703.)

The development of the parts of the limb now referred to, both in its larger features and in its histological characters, is usually somewhat more in advance in the anterior than in the posterior extremities.

Fig. 703.

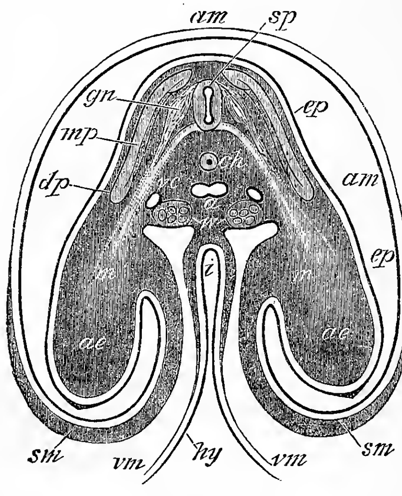


Fig. 703.—Transverse section of the body of the chick at the level of the anterior extremities. (From Remak.)

am, amnion in its cephalic fold; *ep*, epiblast; *sm*, parietal mesoblast; *vm*, visceral mesoblast; *sp*, spinal marrow; *gn*, spinal ganglion and nerve roots; *mp*, muscle-plate; *dp*, dermal plate; *ch*, notochord, with vertebral matrix round it; *a*, aorta (the two uniting into one); *vc*, cardinal veins; *w*, mesentery and Wolffian bodies; *ae*, anterior extremities composed of mesoblast, *m*, and covered with epiblast thickened at the point; *i*, intestinal canal open below into the yolk sac; *hy*, hypoblast.

Attitude and position of the Limbs.—From the manner in which the primary lappet or limb-plate grows from the side of the axial part of the trunk, it is obvious that at first it must present a dorsal and a ventral surface, corresponding respectively with those of the embryo body, and if we trace the subsequent changes which bring out the features of the later form, we shall find them such as to show that the original dorsal aspect is the extensor and the ventral aspect is the flexor surface of the limb; and further that when the distinction of the subordinate parts begins to be established, the thumb and great toe, reckoned in descriptive anatomy as the first of the series, and corresponding with the radial and tibial borders of their respective limbs, are directed forwards or preaxially, while the fifth toes, with the ulnar and fibular borders of their respective limbs, are directed backwards or postaxially.

As development proceeds, the two primary lappets, from being at first simple lateral extensions from the trunk, come to be folded ventrally or against the body of the embryo, the anterior with something of a backward, and the posterior with a forward direction. But they have now also undergone other changes, by which the attitude of the distal segments is affected differently in the two limbs, in this respect, that in the fore-limb the flexure between the proximal and the

middle segments is directed forwards or ventrally, while in the hinder limb it is in the reverse direction, that is backwards or dorsally. In the human body this flexure does not involve any considerable departure from the original relation of the extensor and flexor surfaces to those of the trunk, although in the adult it may appear to do so in consequence of the limb hanging somewhat obliquely in a direction parallel to the main axis of the trunk. But in the hind limb it is obvious that there must be from an early period a certain amount of rotation of the whole limb or from the hip-joint downwards, which brings the extensor surface of the thigh, lower leg and foot forwards, and carries the flexor surface of these parts backwards.

Fig. 704.

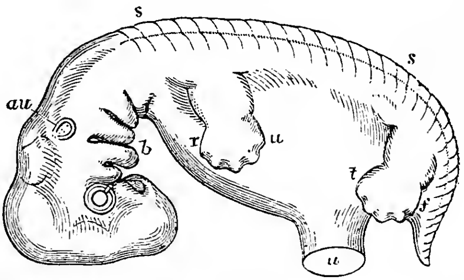


Fig. 704. — DIAGRAMMATIC OUTLINE OF THE PROFILE VIEW OF THE HUMAN EMBRYO OF ABOUT SEVEN WEEKS, TO SHOW THE PRIMITIVE RELATIONS OF THE LIMBS TO THE TRUNK. (Allen Thomson.)

r, the radial (preaxial), and *u*, the ulnar (postaxial, border of the hand and fore-arm ; *t*, the tibial (preaxial), and *f*, the fibular (postaxial) border of the foot and lower leg. (The foot is represented at a somewhat more advanced stage than the rest of the embryo.)

In quadrupeds, however, it is different as regards the fore-limb, for in them, while there is the same kind and degree of rotation in the hind-limb, equal to a quarter of a circle, as in man, there is also a rotation of the humerus outwards, and frequently a forward displacement of the upper end of the radius with more or less complete pronation of its lower extremity, which brings the palmar aspect of the fore-limb towards its original ventral position ; this becoming most completely restored when in the state of extension more or less of the forefoot supports the body on the ground. In this the pollex, like the hallux, is placed towards the mesial side. This rotation of the fore-limb, amounting in all to half a circle, is made up of an outward rotation of the humerus at the shoulder-joint and an inward rotation of the fore-arm at the elbow-joint.

In the development of the several deeper components of the limbs it is to be observed in the first place with respect to the skeleton, that the formation of the bones with their accessory parts takes place by a primary differentiation of the blastema into cartilaginous matrices and fibrous or membranous parts, and the subsequent calcification of the cartilages and subperiosteal ossification, in the manner fully described in the histological part of this volume (p. 101), to which, as well as to the history of the progress of ossification in the several bones, given in the first volume, the reader is referred.

It may be further stated here that in all the bones of the limbs, with the exception of the terminal phalanges, the processes of cartilaginous calcification and true ossification begin at the middle and extend thence towards the ends of the bone-matrices, but in the terminal phalanges these processes commence in the distal ends and proceed from thence inwards upon the rest of the bone-matrices,—a fact of considerable morphological significance with reference to the determination of the homologies of the terminal elements of the limbs in the lower vertebrates. (Dixey, No. 172.)

It may also be mentioned here that it has been found by Henke and Reyher (No. 165) that in the human embryo of the seventh and eighth weeks there is a distinct cartilage, representing the os centrale of animals, placed between the

scaphoid, magnum and trapezium cartilages, but this central cartilage gradually diminishes and passing dorsally disappears in the course of the third month, without either uniting with any of the neighbouring bone-matrices or undergoing ossification.

Muscles.—With respect to the muscles of the limbs, it seems still doubtful whether they proceed directly from the muscle-plates, which it is admitted reach the root of the limbs by their outer edge, or whether they arise locally. It may be that the muscles take their origin in both of these modes, the trunk-muscles which are attached to the limbs being most probably formed in connection with the muscle-plates.

The Joints.—The differentiation of the blastemic tissues into the parts which are to form the joints takes place at the same time that the primary chondrification shows itself for the formation of the bone-matrices, and is coincident also with the commencement of the perichondrium and the fibrous and vascular osteogenic elements. There are at first no joint-cavities, and the fibrous or connective tissue, forming a sort of articular plate between the bone-matrices, may therefore be said to unite them by syndesmosis. But very soon, or in the human embryo of from seven to eight weeks, when chondrification is complete, narrow slits make their appearance in the places of the future joint-cavities, and the fibrous structures retiring from the interior towards the surface, the cavities undergo enlargement into their permanent form,—a process which approaches completion in the human embryo of four months.

The ligaments are developed from the remains of the fibrous matrix, in connection with the earlier perichondrium which becomes converted afterwards into permanent periosteum.

Nerves and Blood-vessels.—The nerves of the limbs probably differ from their other constituents as regards their origin, in this respect, that they are prolonged into the limbs by extension from the nerve-roots which emanate from the spinal marrow. Similarly the blood-vessels of the limbs arise to some extent by prolongation from those of the trunk ; but no doubt there are also many blood-vessels formed locally or within the mesoblastic tissue of the limbs ; and it is not known to what extent the growth of the nerves in the peripheral parts of the trunk and limbs may be due to a similar local development.

IV. EXTERNAL COVERING OF THE BODY AND LIMBS.

The epiblast which is not employed in the formation of the nervous centre or other deeper parts remains as the source of the epidermis and its appendages. This covers all the external surface of the body and penetrates into such cavities as the mouth and nasal fossæ, &c., whose surfaces are in original continuity with it. Besides the two layers distinguished as corneous and mucous in the epidermis, it gives rise to the hairs and nails, and the teeth of mammals, to the feathers of birds and to the scales and horny plates of these or other animals. It is, however, closely united with the subjacent dermoid tissue, from the blood-vessels of which the materials for its formation and that of its appendages are derived.

The true skin or dermis, of a much more complex structure, is formed entirely from mesoblast, and arises in close connection with the muscular plates The fasciæ and connective tissues spring from the same source.

The cellular structure of the sebaceous and sudoriferous glands, and

also of the mammæ, is all of true epiblastic origin; but their blood-vessels, connective tissue, and other superadded parts are derived from mesoblast.

V. FORMATION OF THE HEAD.

The distinction between the head and trunk by the formation of a cervical constriction is a change of comparatively late occurrence, but even long before this constriction appears, the characteristic features of the parts in these three regions have become apparent. The head may be said to consist at first wholly of the cranial part,—the face being developed at a later period from a series of outgrowths or bars which proceed downwards and forwards from the base and front part of the cranium. The head in its primitive cranial form is, of course, covered externally like the rest of the body by the epidermis derived from the epiblast, and between this and the primary medullary wall of the great nervous centre a layer of mesoblast is soon interposed, from which originate the cover-

A Fig. 705. B

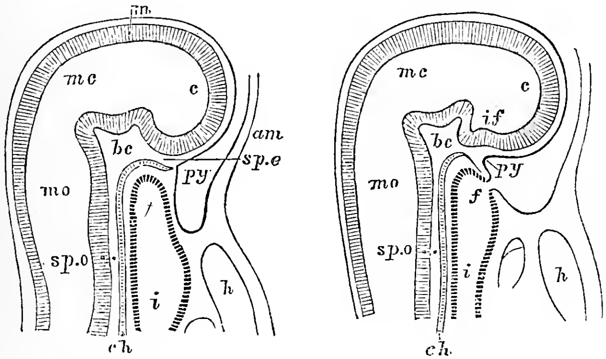


Fig. 705.—Vertical section of the head in early embryoes of the rabbit. Magnified. (From Mihalkovics.)

A. From an embryo of five millimetres long.
B. From an embryo of six millimetres long.
In A, the faucial opening is still closed; in B, it is formed; *c*, anterior cerebral vesicle; *mc*, meso-cerebrum; *mo*, medulla oblongata; *m*, medullary layer; *if*, infundibulum; *am*, amnion; *spe*, spheno-ethmoidal, *bc*, central (dorsum sellæ), and *spo*, spheno-occipital parts of the basis cranii; *h*, heart; *f*, anterior extremity of primitive alimentary canal and opening (later) of the fauces; *i*, cephalic portion of primitive intestine; *ch*, notochord; *py*, buccal and pituitary involution.

ings of the brain, the muscular plates, the cartilaginous and bony elements, the true skin, the connective tissue, blood-vessels, and other components of the more advanced cranial walls. This mesoblast may be regarded as a cephalic prolongation of the protovertebral plates of the trunk, but as we shall see hereafter without undergoing obvious metameric segmentation.

The notochord, as already stated, extends for some distance into the base of the cranium, and is there imbedded in a mass of tissue, the *investing mass* of Rathke, which afterwards becomes the *parachordal* cartilages forming the principal matrix of the future bony walls of the cranial base, as far forward as the sella turcica. From this place the

cartilaginous rudiments are continued forwards in two more or less united bars named the *trabeculæ cranii* by Rathke, and having a space between them posteriorly which is afterwards the seat of the pituitary gland. The trabeculæ stretch forward until they reach the region of the olfactory pits, and enclose that depression on each side with the nasal cartilages developed from them in front.

The basis cranii in this view may be considered as composed of a posterior chordal part the *occipito-sphenoid*, and an anterior achordal part the *spheno-ethmoid*.

The facial part of the head, on the other hand, is mainly composed of plates or bar-like growths from the front and sides of the base of the cranium which may be distinguished as of two sets, according as they are placed in front of or behind the mouth or buccal cavity. But the mouth as we know it at a later period, either in the form of a cavity of the face or as the anterior aperture of the alimentary canal, has at first no existence, the anterior extremity of that canal being closed by the original cephalic fold of the blastoderm, and the forehead, nose, cheeks, jaws and lips being as yet entirely absent.

Fig. 706.

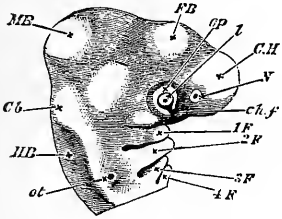


Fig. 706.—Side view of the head of an embryo-chick of the third day. (From Balfour.)

CH, cerebral hemispheres; *FB*, thalamencephalon; *MB*, midbrain; *Cb*, cerebellum; *HB*, medulla oblongatæ; *N*, nasal pit; *ot*, auditory vesicle not yet closed externally; *op*, optic vesicle, with *l*, the lens, and *chf*, the choroidal fissure (in mesoblast); 1*F*, the first visceral fold or plate, the superior maxillary fold slightly indicated above it; 2, 3, 4*F*, the second, third and fourth visceral plates with the visceral clefts between them.

The mouth therefore is formed by a transverse cleft or depression between facial bars or plates, and owes its production as a cavity more to the development outwards of these bars, than to the depression inwards of the anterior cranial wall in which it is situated. The later formed buccal aperture or communication with the pharynx is produced only on the fifth day in the chick by a wearing through or absorption of the epiblast and hypoblast of the original cephalic fold at the fauces or anterior part of the primitive alimentary cavity. The facial plates which are in front of the future mouth, and are sometimes named *preoral arches*, consist mainly of the single or median fronto-nasal plate, and in lateral pairs of the external nasal and maxillary plates, the last constituting the basis of the upper jaw, and arising in connection with the mandibular next mentioned.

The subcranial plates or bars which lie behind the mouth, and are, therefore, named *postoral arches*, consist in the amniota of five pairs of wall plates, meeting each other ventrally below the mouth and pharynx. The first of these, named mandibular, is that in which the lower jaw is formed. The second pair of bars is the seat of development of the upper part of the hyoid bone, and is therefore named hyoid. The three following bars correspond in their relations with the most anterior of the arches which support the developed gills of aquatic vertebrates, and may therefore be strictly named branchial,—a name which was not inappropriately given to the whole series by their discoverer, Rathke.

The skull like the rest of the skeleton is at first entirely membranous;

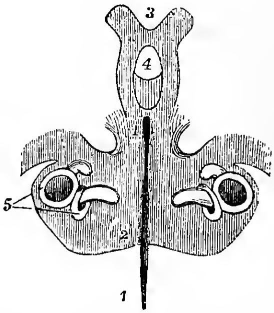
chondrification then takes place in certain parts of the blastema ; and ossification follows in the third stage, partly in the cartilaginous and partly in the membranous matrices.

1. **The Cranium.**—The basal portion of the cranium, as already stated, consists primarily of two fundamental parts. Of these the posterior is distinguished, as before stated, by the presence of the prolongation of the notochord within it as far forward as the part of the skull which afterwards becomes the dorsum sellæ. This portion, comprehending the parachordal plates which surround the anterior extremity

Fig. 707.—The lower or cartilaginous part of the cranium of a chick of the sixth day. (From Huxley.)

1, 1, chorda dorsalis; 2, the shaded portion here and forwards is the cartilage of the base of the skull; at 2, the occipital part; at 3 the prolongations of cartilage into the anterior part of the skull called *trabeculæ cranii ;* 4, the pituitary space ; 5, parts of the labyrinth.

Fig. 707.



of the notochord, contains the matrix of the future basi-occipital and basi-sphenoid cartilages. By its later extension to the sides, it forms the matrix of the exoccipitals and the periotic mass of cartilage which surrounds the primary auditory vesicles. The main part extends forward below the posterior and middle primary encephalic vesicles, ending at the pituitary fossa.

The *spheno-ethmoid* portion of the basis cranii contains the matrix of the presphenoid, and the septal-ethmoid cartilages. It is mainly produced in connection with the trabeculæ cranii, which are in direct continuity with the anterior part of the parachordals.

The trabecular part lies below the anterior encephalic vesicle, and becomes greatly modified in connection with the expansion of the cerebral hemispheres and the development of the nasal fossæ and mouth, together with the other parts of the face.

The three principal sense organs, it may here be stated, the nose, eye, and ear, formed in connection with their several primary nervous parts derived respectively from the cerebral hemispheres, the thalamencephalon, and the third primary vesicle, are interposed between the rudimentary parts of the head as follows, viz. : the nose between the frontal, ethmoid and maxillary ; the eye between the frontal, sphenoid, ethmoid and maxillary ; and the ear between the basi-occipital, exoccipital and alisphenoid. Of these the auditory vesicles come to be surrounded by a thick cartilaginous wall which is continuous with the parachordal cartilage and seems to take the place of that cartilage as a part of the general cranial wall.

While the base of the cranium, to the extent already mentioned, is cartilaginous in its origin, the lateral and upper walls are chiefly of membranous formation, as in the squama occipitis, the squamo-zygomatic of the temporal, the parietal and the frontal bones.

The membranous tissue in which these flat bones of the cranial vault are formed is regarded by Kölliker as of dermal origin, and the bones as belonging to the group of investing bones. Their formation is however

in part supplemented by the extension upon them from below of a plate of cartilage which is placed internally to the membranous matrix.

The trabeculæ stretch forward to the anterior extremity of the head, and maintain the foremost place in the seat of the nasal cartilages and external apertures of the nose. Behind these the coalesced trabeculæ

Fig. 708.

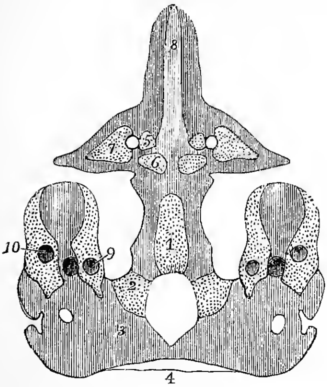


Fig. 708.—View from below of the cartilaginous base of the cranium with its ossific centres in a human fœtus of about four months. (From Huxley, slightly altered.)

The bone is dotted to distinguish it from the cartilage, which is shaded with lines. 1, the basilar part, 2, the condyloid or lateral parts, and 3, 4, the tabular or superior part of the occipital surrounding the foramen magnum ; 5, centres of the presphenoid on the inside of the optic foramen ; 6, centres of the post-sphenoid ; 7, centres of the lesser wings or orbito-sphenoid ; 8, septal cartilage of the nose ; 9 and 10, parts of the labyrinth.

form a narrow ethmo-vomerine cartilage, the nasal septum, round the back of which the vomer is formed as a bony splent covering ; while in the hinder lyre-shaped interval of the separated trabeculæ is placed the infundibulum in connection with the pituitary body.

From the side of the presphenoid cartilage the matrix of the orbito-sphenoids or lesser wings, containing the optic foramina, is developed : and from the sides of the basi-sphenoid proceeds the matrix of the greater wings, which are also cartilaginous in their origin.

In the periotic or cartilaginous rudiment of the temporal bone three centres of formation are distinguished by Huxley, viz.: 1. *Opisthotic*, or that surrounding the fenestra rotunda and cochlea ; 2, *prootic*, or that which encloses the superior semicircular canal ; and 3, *epiotic*, or that

Fig. 709.

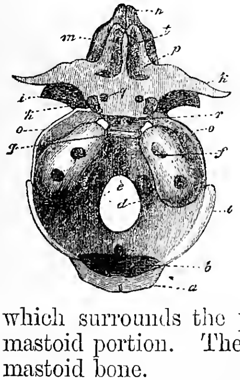


Fig. 709.—Basilar part of the primordial cranium of a human fœtus of three months, seen from above. (From Kölliker.)

a, upper half of the squama occipitis ; *b*, lower half of the same ; *c*, cartilaginous plate extending into it ; *d*, (in the foramen magnum) the exoccipital ; *e*, basi-occipital ; *f*, petrous, with the meatus auditorius internus ; *g*, dorsum sellæ, with two nuclei belonging to the basi-sphenoid bone ; *h*, nuclei in the anterior clinoid processes ; *i*, great wing nearly entirely ossified ; *k*, small wings ; *l*, crista galli ; *m*, cribrethmoid ; *n*, cartilaginous nose ; *o*, strip of cartilage between the sphenoid and the parietal ; *p*, osseous plate between the lesser wings and the cribriform plate.

which surrounds the posterior semicircular canal and extends into the mastoid portion. They soon unite into one so as to form the petro-mastoid bone.

Here it may be stated that, in addition to the parts of the skull before-mentioned, the ethmo-turbinals and cribriform plate, the styloid process and the three auditory ossicles are of cartilaginous origin ; but the

tympanic ring, the nasal, maxillary and other facial bones are all formed in membrane. To these, however, we shall recur hereafter.

In the cranium of the human embryo chondrification begins in the basilar portion in the fourth and fifth weeks, and is nearly completed for the principal parts by the eighth week, soon after which in the course of the tenth week cartilaginous ossification sets in. But in some of the membrane bones, as for example in the lower jaw, ossification begins at a much earlier date, probably in the sixth week.

The form of the head is greatly modified at an early period of development by the cranial flexure as well as by the changes which accompany the development of new parts.

The Cranial Flexures.—The earliest and the most important of the cranial flexures is that, previously mentioned, which takes place at the anterior extremity of the notochord and in the region of the mid-brain or middle encephalic vesicle. At this place the medullary tube, and the substance forming the wall of the cranium especially, undergo a sudden bending downwards and forwards, so as to cause the projection of the thickened cranial base in a marked manner upwards. This coincides with the place where the parachordals and the trabeculæ meet, and where inferiorly the pituitary body, and superiorly the infundibulum come into close relation.

Fig. 710.

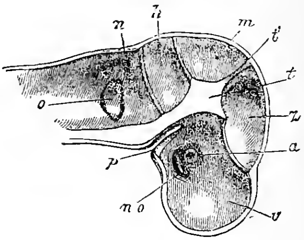


Fig. 710.—Longitudinal section through the head of an embryo of four weeks. (From Kölliker.) $\frac{10}{1}$.

v, anterior encephalic vesicle, cerebral portion; *z*, inter-brain; *m*, mid-brain; *h*, cerebellum; *n*, medulla oblongata; *no* and *a*, optic vesicle; *o*, auditory depression; *t*, centre of basi-cranial flexure; *t'*, lateral and hinder parts of tentorium; *p*, the fold of epiblast which forms the hypophysis cerebri.

Above and behind this, the mid-brain gives greatest prominence to the part of the cranium occupied by it, a feature which remains characteristic of the embryo head for a considerable time.

The great cranial flexure thus marks the division between the strictly basi-cranial, or occipito-sphenoidal, and the basi-facial, or spheno-ethmoidal part, the chorda terminating between those two portions of the cranial base, with a thinner pointed part. Here the end of the chorda is bent downwards and forwards, and terminates in the post-sphenoid body, at the dorsum sellæ.

Other flexures also occur in connection with the development of the brain, but these do not affect materially the external form of the head. In man and the higher mammals the greatest modification of that form results primarily from the expansion of the cerebral hemispheres, and secondarily from the formation and proportional increase in the size of the jaws and other parts of the face.

1. **The Face.**—The formation of the facial part of the head takes place superficially by the downward and forward growth from the front and base of the simple cranium of the median *fronto-nasal* and the lateral *maxillary and mandibular* plates, and more deeply by the development of parts in connection with the cranio-facial axis, which is formed by the spheno-ethmoid extension of the trabeculæ

cranii. These formative changes are of a very complex kind, and comprehend the production of the external nose, the lips and cheeks, the jaws and palate, the deeper nasal fossæ and their labyrinth, the buccal cavity and the orbits, the auricle, auditory meatus and tympano-Eustachian passages, together with the various cavities of the bones in communication with the involuted nasal passages, such as the ethmoid, maxillary, sphenoid and frontal sinuses.

These parts all arise mainly in mesoblastic tissue, but are covered externally by epiblast, or are lined internally by that layer, excepting the tympano-Eustachian passage, which has a hypoblastic lining. The basi-facial axis is at first necessarily very short, as it lies only below the undeveloped first cerebral vesicle, but it speedily assumes greater proportions as it is elongated forward with the enlargement of the cerebral hemispheres and the simultaneous development of the nasal and buccal fossæ.

The nasal fossæ take their origin in the form of two simple depressions, the *primary olfactory* or *nasal pits*, which appear on the lower

Fig. 711.

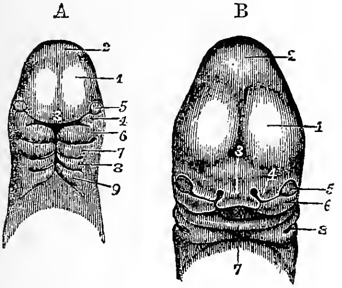


Fig. 711.—Cranium and face of the human embryo, seen from before. (From Ecker.)

A, from an embryo of about three weeks: 1, anterior cerebral vesicles and cerebral hemispheres; 2, inter-brain; 3, middle or fronto-nasal process; 4, superior maxillary plate; 5, the eye; 6, inferior maxillary or mandibular plate (first postoral); 7, second plate; 8, third; 9, fourth, and behind each of these four plates their respective pharyngeal clefts. B, from an embryo of five weeks: 1, 2, 3, and 5, the same as in A; 4, the external nasal or lateral frontal process; 6, the superior maxillary plate; 7, the mandibular; ×, the tongue; 8, the first pharyngeal cleft, which becomes the auditory passage.

surface of the wall of the anterior cerebral vesicle at a very early period when no other parts of the face have yet been formed. But the trabecular part of the cranial wall, now extending forwards and doubling itself at its anterior extremity, curves round both the nasal pits from the inside and above, so as to cover them in some sort with a dome (Parker), in connection with which are afterwards formed the forepart of the septum and the lateral nasal cartilages. The nasal pits have at first no connection with the mouth, which forms a transverse depression in the lower and hinder part of the future face; but later, or by the fifth week in the human embryo, these cavities are brought into communication by the formation of the nasal grooves which run backwards one from each olfactory pit into the mouth, and at the same time the nasal fossæ begin to extend themselves upwards as narrow passages on each side of the enlarging septum, the lower part of the fossæ being still left in open communication with the buccal cavity.

Fronto-nasal Plate.—The external nose owes its origin to the development of the fronto-nasal plate, previously mentioned, which forms a broad median lappet in the fifth and sixth weeks of the human embryo, descending from the front of the cranium between the two large ocular vesicles as far as the transverse buccal cleft. It is free in front and inferiorly, but behind it is in union with the parts developed from

the trabecular axis. Its lower border encloses the nasal pits which come to form deep notches in it, and it is thus divided into a median and two lateral nasal processes. The central division forms the prominent part of the future nose with its *columella* below, and its further prolongation downwards gives rise to the *lunula* or central part of the upper lip; while the parts outside the nasal notches, *the external nasal processes*, receding somewhat, reach the orbital fissure, and are the source, later, of the alæ of the nose.

The further development of the nose consists mainly in the formation of the deeper parts, such as the septum, cribriform plates, and the labyrinth or turbinal portions, which will be noticed in connection with the olfactory organ. Here we have only to do with its relation to the face and mouth.

The Mouth.—The buccal cavity arises as a wide cleft or depression in the lower part of the face, having above it the fronto-nasal process in the middle, and the superior maxillary processes on each side, and

Fig. 712.

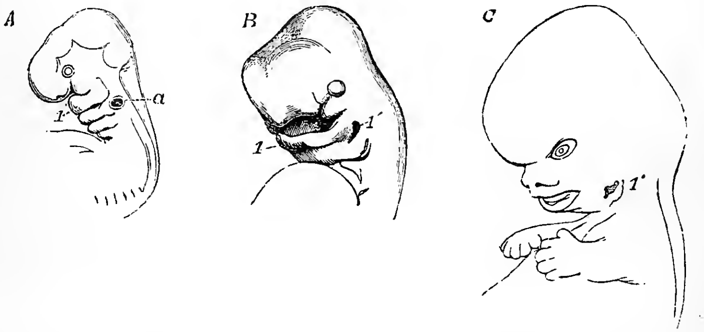


Fig. 712.—Outlines showing the early changes in the form of the head of the human embryo.

A, profile view of the head and fore part of the body of an embryo of about four weeks (from nature, $\frac{10}{1}$) : *a*, the auditory vesicle; 1, mandibular arch, and behind this are seen the three following arches with the corresponding pharyngeal clefts. *B*, embryo of about six weeks (from Ecker, $\frac{5}{1}$); 1, the lower jaw: 1′, the first pharyngeal cleft, now widening at the dorsal end, where it forms the meatus externus; the second cleft is still visible, but the third and fourth clefts are closed and the corresponding plates have nearly disappeared. *C*, from a human fœtus of nine weeks (from nature, $\frac{3}{1}$); the features of the face are now roughly formed; the meatus is forming in the dorsal end of the first pharyngeal cleft, and the auricle is beginning to rise from its outer border.

below it the first pair of visceral arches or mandibular plates, which meet each other in the middle, and are continuous round the outer angles of the mouth with the maxillary processes; the deepening of the buccal cavity itself being mainly due to the outward development of these several processes.

The primitive mouth (*stomodæum*) is therefore lined entirely by epiblast, and is separated from the fore-end of the pharynx by this layer, as well as by the inflection of the visceral mesoblast and the hypoblast which close that cavity anteriorly. The establishment of a communication between the mouth and pharynx by the wearing through of the several blastodermic layers named, in the form at first of a vertical slit,

takes place on the fifth day in the chick, and probably at the eighth or ninth week in the human embryo. To this change, which gives rise to the aperture of the fauces, reference will again be made in the history of the development of the alimentary canal. From what has been said previously, it is apparent that the upper lip is formed in part by the fronto-nasal and maxillary plates which are at first separated by the orbital fissures, and that the lower lip is a part of the mandibular plates. The integrity of the upper lip is established by the inward advance of the superficial part of the lateral maxillary processes, which, coalescing with both the internal and external nasal processes, close in the nasal notches inferiorly as the nostrils, and obliterate in great part the orbital fissures,

Fig. 713.

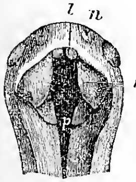


Fig. 713.—Head of human embryo of eight weeks, seen from below, the lower jaw having been removed. $\frac{4}{1}$. (From Kölliker.)

n, the external nasal apertures; *i*, premaxillary process, and outside this the internal nasal aperture; *m*, palatal process advancing from the side to form the partition between mouth and nose; *p*, common cavity of the nose, mouth and pharynx.

leaving only more deeply within them the lachrymal canals or nasal ducts. While the upper lip is thus completed superficially, a deeper development and union of the maxillary and intermaxillary matrices occurs, which leads to the completion of the alveolar arch.

The separation of the cavity of the mouth strictly so called from the nasal fossæ, is effected by the development of the palatal or pterygo-palatal processes of the maxillary plate, which advancing inwards from the two sides meet and coalesce with each other and with the septum descending from above in the middle line. But this median union does not in the same form extend to the anterior part which is occupied by the intermaxillary process; for here the maxillo-intermaxillary cleft is double, and, when the union of the opposite parts takes place, the naso-palatine canal is left as the vestige of the previous fissures.

Fig. 714.

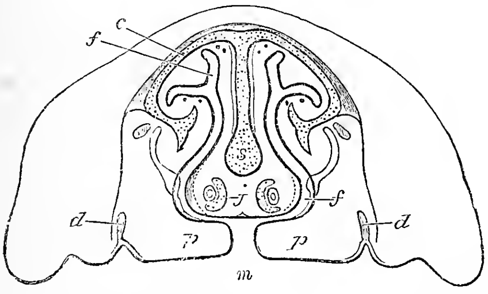


Fig. 714.—Outline of a transverse vertical section through the nose and upper jaws of a sheep's embryo with open palate. (From Kölliker) slightly magnified.

The lower jaw and tongue are removed; *m*, the mouth; *d*, dental germs; *p*, the palate plates approaching each other in the middle; *f*, the nasal fossæ; *c*, nasal cartilage; *s*, septal cartilage; *j*, the two organs of Jacobson with their cartilages internally.

The median union of the palate begins in front about the eighth week in the human embryo, and reaches the back part, when completed, in the ninth and tenth weeks. There are thus formed the hard and soft palates as the floor of the lower or respiratory part of the nasal fossæ,

leading posteriorly into the pharynx, and the roof of the proper buccal cavity. The malformations of double hare-lip and maxillo-intermaxillary clefts, which usually accompany it on one or both sides, together with that of the single or median cleft palate in its various degrees, receive an interesting explanation from the study of the developmental phenomena now referred to.

It is in connection with the lower part of the septum and intermaxillary plate that there are found at an early period in the human embryo as well as in that of other mammals the rudiments of the **Organ of Jacobson** and the inferior internal nasal cartilages which surround them externally (see fig. 714).

It may further be mentioned at this place that from the roof of the mouth at a very early period, as by the third or fourth week in the human embryo, there is formed the diverticulum lined by epiblast, which in its combination with the infundibulum and farther development, gives rise to the pituitary body (see later, p. 831).

In the superficial part of the maxillary plates are formed the superior maxillary and malar as membrane or investing bones, and on the inside of the orbit in connection with the nasal duct the lachrymal bones.

There is a marked difference between the bones which arise in connection with the trabeculæ, such as the pre-sphenoid, orbito-sphenoid, septal ethmoid, cribriform and ethmo-turbinal, which have all cartilaginous matrices, and those which are of membranous origin and have an investing character, such as the nasal, lachrymal, vomer, internal pterygoid, palatal, superior maxillary, malar and mandibular bones of the face. It is, however, an interesting fact (Kölliker) that the various sinuses which come to occupy places within some of the cranial and facial bones, such as the ethmoid, maxillary, sphenoid and frontal, all arise by extension of the epiblastic lining of the nasal passages, and are preceded by the formation of cartilaginous capsules, within each of which the epiblastic extension is situated, and that these epiblastic and cartilaginous capsules make their way gradually into the interior of the respective bones afterwards occupied by the sinuses, the bones being gradually hollowed out by absorption to receive them. In this process the ethmoid sinuses are the earliest to be formed, beginning at the sixth month in the human embryo; the maxillary follow very soon, or nearly at the same stage, but continue to grow for a long time. The sinuses do not penetrate the sphenoid till about the seventh year, having peculiar relations with the bones of Bertin (see vol. I., p. 72), and the frontal sinuses are the latest in appearing, not having made much progress till the age of puberty, when they expand rapidly, and when also all the others undergo a greater extension.

2. **Postoral Visceral Arches—Branchial Arches.**—The formation of the lateral and lower parts of the face, including the mouth and lower jaws, the hyoid apparatus, the auricles and tympano-Eustachian passages, is intimately connected with the development of the subcranial pairs of processes which are most appropriately named the *Visceral Arches*, as enclosing the mouth and the anterior or pharyngeal portion of the primary alimentary cavity. The visceral arches now referred to were first described by Rathke in 1825, (No. 173,) and from their general homology with the arches of the gills in aquatic animals were named by him the branchial arches. Their development was subsequently very fully investigated by Reichert (1837, No. 174).

In the amniota the postoral visceral arches are four, or, according to some, five in number. The first or anterior of these plates, which forms the posterior margin of the mouth, and is named *mandibular*, is the seat of formation of the lower jaw; the second, named *hyoid*, gives origin in part to the hyoid apparatus; the third arch, in which the remainder of the hyoid bone is formed, and which may be named *thyro-hyoid*, corresponds to

the first of those which in aquatic animals undergoes full branchial development, but which in the amniota, like the two following it, never bears gills.

The fourth and fifth arches have no special names, but might be termed post-hyoid or cervical, as being situated in the place where the elongation of the neck occurs at a later period,—a process which gives rise to some of the peculiar features familiar to anatomists as characterising the parts occupying the cervical region.

Visceral Clefts.—Behind each of these visceral arches there is placed on each side a cleft which runs through the wall of the body from the external surface into the cavity of the pharynx, thus bringing epiblast and hypoblast into continuity. The first of these clefts, which from its position may be named *hyo-mandibular*, is afterwards the seat of the formation of the Eustachian passage and cavity of the tympanum

Fig. 715.

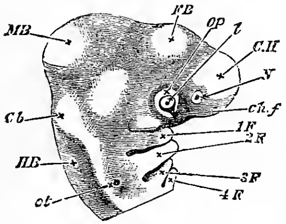


Fig. 715.—Side view of the head of an embryo-chick of the third day. (From Balfour.)

CH, cerebral hemispheres ; *FB*, vesicle of the third ventricle ; *MB*, mid-brain ; *Cb*, cerebellum ; *HB*, medulla oblongata ; *N*, nasal pit ; *ot*, auditory vesicle not yet closed externally ; *op*, optic vesicle, with *l*, the lens, and *ch.f*, the orbital fissure (in mesoblast) ; 1*F*, the first visceral fold or plate, the superior maxillary fold slightly indicated above it ; 2, 3, 4*F*, the second, third, and fourth visceral plates with the visceral clefts between them.

internally, while the meatus auditorius is developed externally round the dorsal part of the cleft by the outgrowth of the neighbouring parts of the two arches ; the membrana tympani growing up between them. The external auricle is developed from the integument behind the meatus. The three remaining clefts, which represent branchial apertures of aquatic animals, are all closed in the amniota at an early period, corresponding to the sixth or seventh week in the human embryo.

In some of the lower vertebrates, as in the elasmobranchs and cyclostomes, the hinder branchial arches are more numerous than in other animals, and in some the hyoid arch possesses a developed gill. In aquatic animals generally the gill arches have cartilaginous bars, but in man and mammals it is only in the three first visceral arches, that is, the mandibular, hyoid and thyro-hyoid, that cartilaginous bars are formed.

Through each of the visceral arches there runs a considerable arterial vessel, which is one of the five pairs of vascular arches formed by the division of the aortic bulb, and which in the embryoes of amniota reunite dorsally, without subdivision into branchial vessels, to form the aorta (see Vascular System, p. 868).

It is an interesting fact stated by Balfour that in the early stages of development of the branchial plates in elasmobranchs there is in the outer part of each of them a cavity extending from the ventral to the dorsal ends, which he regards as having been derived by extension from the general body-cavity in the same manner as occurs in the vertebral somites of the trunk of the body ; and further that muscle-plates are formed round these head cavities, which probably furnish the rudiments of a certain number of the head muscles.

Farther Destination of the Visceral Arches.—Some of the remaining facts respecting the development of the visceral arches will be most conveniently described along with those relating to the formation of

the ear and other organs with which they are associated. Here it will be sufficient to state shortly the principal destination of each of them,

The cartilage of the first or mandibular visceral arch has long been known as the *cartilage of Meckel*, which occupies the deeper part of the arch from a very early period, and, attaining considerable size, remains visible in the human fœtus up to the sixth or seventh month. Its proximal portion is now known to be converted into the *malleus* of mammals, and into the homologous *quadrate* bone of reptiles and birds.

In mammals the lower jaw, corresponding mainly with the dentary bone of other animals, is developed at a very early period first from membrane outside Meckel's cartilage; but it is also partially incorporated with those cartilages at their lower or distal part where they meet each other in the symphysis. A part of Meckel's Cartilage between the jaw and the malleus is converted into the so-called internal lateral ligament of the jaw.

Fig. 716.

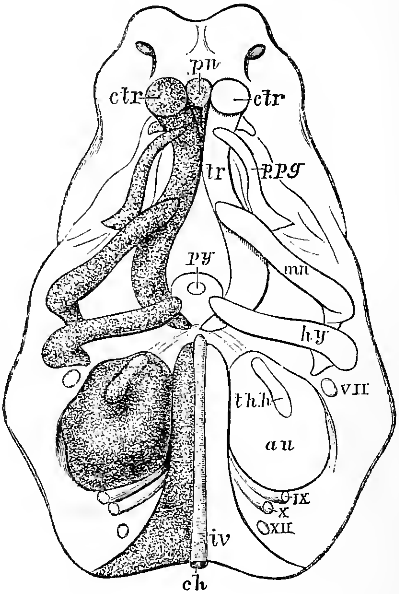


Fig. 716.—Plan of the skull, &c., of the embryo pig, seen from below. Magnified ten diameters. (From Parker.)

tr, cartilage of the trabeculæ; *ctr*, cornua trabecularum; *pn*, prenasal cartilage; *ppg*, pterygo-palatine cartilage; *mn*, the mandibular arch with Meckel's cartilage; *au*, the auditory vesicle; *hy*, the cerato-hyoid arch; *thh*, the thyro-hyoid; *py*, the pituitary fossa; *ch*, the notochord in the cranial basis, surrounded by the parachordals (*iv*); VII, facial nerve; IX, glosso-pharyngeal; X, pneumogastric; XII, hypoglossal nerve.

The second or hyoid visceral arch is originally closely united with the first arch at its cranial extremity below the auditory capsule. It contains in its proximal part the cartilaginous matrix of the incus, which becomes articulated with the head of the malleus formed in the adjacent proximal part of the mandibular arch. The remainder of this cartilaginous bar forms the tympano-hyal and styloid processes, the stylo-hyoid ligament, and the lesser wings of the hyoid bone (cerato-hyal).

The third visceral arch or thyro-hyoid gives rise, by its cartilaginous matrix, to the great wings and body of the hyoid bone. It supports the rudiment of the thyroid cartilage, and is closely connected with the development of the larynx.

The fourth and fifth arches, as already remarked, may be considered as belonging to the neck rather than to the head. The congenital fissures of the neck which have been observed as a malformation, and which usually open externally far down in that region, may be due to

the persistence of one or more of the branchial clefts, much drawn out by the cervical elongation.

The tongue is formed, according to Kölliker, in connection with the three first visceral arches, but mainly with the mandibular. Its covering

Fig. 717.

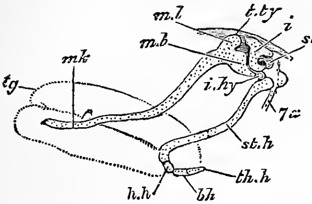


Fig. 717.—SIDE VIEW OF THE MANDIBULAR AND HYOID ARCHES IN AN EMBRYO PIG OF $1\frac{1}{3}$ INCH IN LENGTH. (From Balfour, after Parker.)

tg, tongue ; *mk*, Meckel's cartilage ; *ml*, body of malleus ; *mb*, its manubrium or handle ; *t.ty*, tegmen tympani ; *i*, incus ; *st*, stapes ; *i.hy*, inter-hyal ligament ; *st.h*, stylo-hyal cartilage ; *h.h*, hypohyal ; *bh*, basibranchial ; *th.h*, rudiment of first branchial arch ; *7a*, facial nerve. See also fig. 745, p. 839.

is derived from the epiblast of the mouth, its muscular substance probably proceeds from the muscle-plates of the visceral arches, and it rests by its base on the mesial process of the third arch, the basihyoid element.

Relation of Developmental Facts to the Morphology of the Head.—It may be freely admitted that there is no primary segmentation of the formative elements of the head similar to the division of the vertebral or mesoblastic somites of the trunk; and yet there are not wanting proofs that the development of the head takes place in its earlier phases on essentially the same plan, and from the same blastodermic elements as the axial part of the trunk; while there are also sufficient grounds for recognising in the later stages of the formation of the cartilaginous matrices, and in the ossification of the bones, indications of some degree of segmentation of the cranial and facial elements.

These indications are to be found mainly in 1, the prolongation of the notochord and its parachordal investment from the vertebral axis of the trunk into the cranial base; 2, the enlargements of the notochord at certain places corresponding with the later separation of the bones; 3, the division of the visceral arches and the extension of the body cavity into their substance, together with the formation of muscle-plates in each of them; 4, the general similarity in the relations of the cranial and facial bases and the neural arches to the nervous centre and the issue of the nerves on the one hand, and of all these to the visceral or alimentary cavity on the other. But while these considerations would seem to indicate a morphological correspondence between cephalic and vertebral rudiments, much is still wanting to fill up the details of the comparison between them; and, admitting the serial homology to exist, the number of metameric somites or divisions of the head is not as yet by any means determined.

II. DEVELOPMENT OF THE NERVOUS SYSTEM.

It is one of the most important generalisations resulting from modern embryological inquiry, as has been well remarked by Balfour, that all the organs of the nervous system take their origin from the epiblast, or from the same source as the cuticular covering of the body. And this fact is not confined to vertebrate animals, but is universal throughout the whole of the Metazoa.

I. THE CEREBRO-SPINAL CENTRE.

In Vertebrates the first of these organs to appear is the great nervous centre comprising the brain and spinal cord in their primary rudimentary form of a simple medullary tube (as previously stated at p. 749); and

it is now ascertained that while the central organs are produced by an involution and rapid growth of the epiblast in the line of the vertebral axis of the body, the roots and part at least of the peripheral nerves are developed by secondary extension from the primary medullary centre.

Fig. 718. OUTLINE FROM ABOVE OF THE EMBRYO CHICK IN THE FIRST HALF OF THE SECOND DAY.

1 to 2, the three primary encephalic vesicles enclosed in front and at the sides by the cephalic fold; 3, the hinder extremity of the medullary canal dilated into a rhomboid space in which is the primitive trace; 4, 4, seven proto-vertebral somites.

Fig. 719.—EMBRYO OF THE DOG MORE ADVANCED, SEEN FROM ABOVE. (After Bischoff.)

The medullary canal is now closed in; *c*, the anterior encephalic vesicle; *o*, the primitive optic vesicle; *au*, the primitive auditory vesicle opposite the third encephalic vesicle; *am*, the cephalic fold of the amnion; *ov*, the vitelline veins entering the heart posteriorly; *pv*, the protovertebral somites.

Fig. 718.

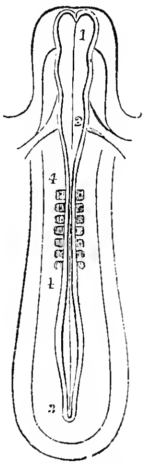
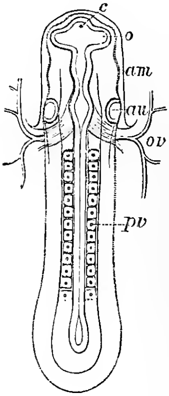


Fig. 719.

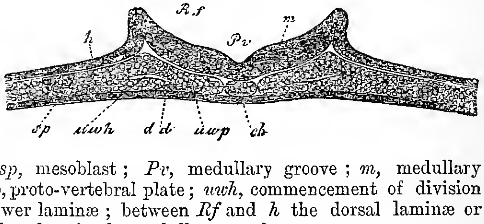


But it is not yet fully ascertained whether the whole of the peripheral nerves are derived from this source or are formed by secondary differentiation from blastema in the more remote seats of their origin.

From what has been previously stated it will have been seen that the rudiment of the cerebro-spinal nervous centre is formed more immediately from the thickened medullary plates of the involuted epiblast, the ridges of which, rising from the surface of the blastoderm, become united dorsally along the middle line so as to close in a hollow medullary tube of a cylindrical form. This tube is wider at its anterior or cephalic extremity, and this dilated portion becomes divided by partial constrictions, first into two, and very soon after into three *primary cerebral or encephalic vesicles*, which represent anterior, middle and posterior

Fig. 720.—TRANSVERSE SECTION THROUGH THE EMBRYO OF THE CHICK AND BLASTODERM AT THE END OF THE FIRST DAY. MAGNIFIED FROM 90 TO 100 TIMES. (From Kölliker.)

Fig. 720.



h, epiblast; *dd*, hypoblast; *sp*, mesoblast; *Pv*, medullary groove; *m*, medullary plates; *ch*, chorda dorsalis; *uwp*, proto-vertebral plate; *uwh*, commencement of division of mesoblast into its upper and lower laminæ; between *Rf* and *h* the dorsal laminæ or ridges which by their approximation close in the medullary canal.

primary divisions of the brain. The spinal portion retains a more uniform cylindrical shape, excepting towards the caudal extremity, where it is longer in being formed, and remains for a time a flat open rhomboidal dilatation. The continuous cavity enclosed within the primitive medullary tube is the same with that which, variously modi-

fied, afterwards constitutes the central ventricles of the brain and canal of the spinal cord.

The formative cells composing the medullary substance are at first

Fig. 721.

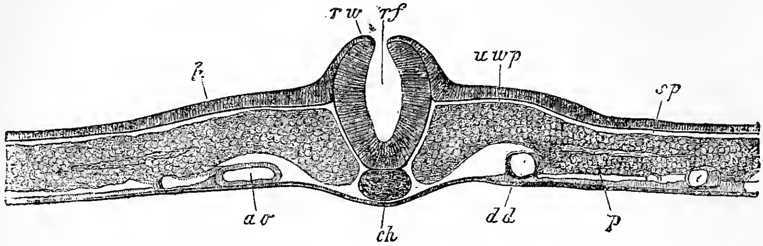


Fig. 721.—Transverse section of an embryo chick of the latter half of the second day, at the place where the vertebral somites cease. $\frac{83}{1}$. (From Kölliker.)

rw, dorsal ridges ; *rf*, medullary groove, or canal beginning to close ; *uwp*, proto-vertebral plate ; *sp*, lateral plate of the mesoblast ; *h*, epiblast ; *dd*, hypoblast ; *ao*, primitive double aorta ; *sp*, commencement of division of the mesoblast which forms the body-cavity.

spherical, but they afterwards become elongated and spindle-shaped, and increase rapidly by multiplication. They represent at first the grey substance, or the nerve-cells and non-medullated fibres. The

Fig. 722.

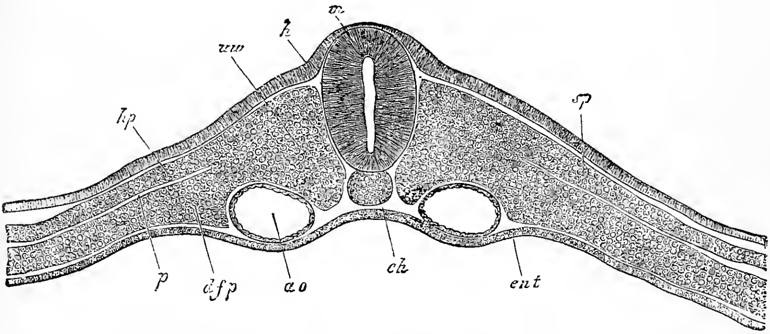


Fig. 722.—Transverse section of the embryo chick in the latter half of the second day, in the region of the proto-vertebræ. $\frac{106}{1}$. (From Kölliker.)

m, medullary tube ; *h*, epiblast now separated from the medullary inflection ; *uw*, proto-vertebral mass ; *hp*, parietal or somatic mesoblast ; *dfp*, visceral mesoblast ; *p*, pleuro-peritoneal or body-cavity between these two layers ; *ch*, notochord ; *ao*, aorta still double ; *ent*, hypoblast.

cylindrical cells which, from the first, line the whole canal, remain permanently in some parts of it, and frequently present the ciliated structure.

THE SPINAL CORD.

The internal grey substance of the spinal cord is first formed ; the white substance is produced later on the exterior. The sides acquire considerable increased thickness, while the dorsal and ventral parts

remain comparatively thin, so that the cavity assumes in section the appearance of a slit, which becomes gradually narrower as the lateral thickening increases; and at last the opposite surfaces uniting in the middle divide the primary central canal into an anterior or lower and posterior or upper part (see figs. 724 and 725).

The lower of these divisions becomes the permanent central canal, the upper or dorsal is afterwards so far obliterated that it is filled with a septum of connective tissue belonging to the pia mater, and becomes the posterior fissure of the cord (in human anatomy) (Lockhart Clarke, No. 188).

In birds and mammals there is no distinction to be seen at first between the outer or corneous layer of the involuted epiblast and the cells which by their increase more immediately constitute the medullary plates. In batrachia, however, the dark colour of the corneous layer shows it to be distinct from a deeper layer which is the more strictly nervous. In Osseous fishes, and some other animals, there is no open medullary groove or canal at first, but an involution of a solid column of epiblast, which subsequently becomes hollow for the formation of a ventricular cavity.

Fig. 723.

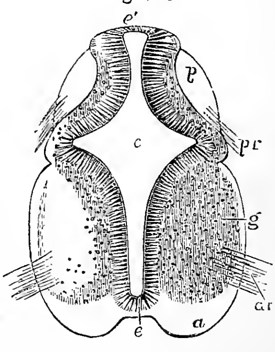


Fig. 723.—Transverse section of the cervical part of the spinal cord of a human embryo of six weeks. (From Kolliker.) $\frac{30}{1}$

This and the following figure are only sketched, the white matter and a part of the grey not being shaded in. *c*, central canal; *e*, its epithelial lining, at *e* (inferiorly), the part which becomes the anterior commissure; at *é* (superiorly), the original place of closure of the canal; *a*, the white substance of the anterior columns, beginning to be separated from the grey matter of the interior, and extending round into the lateral column, where it is crossed by the line from *g*, which points to the grey substance; *p*, posterior column; *ar*, anterior roots; *pr*, posterior roots.

The masses of grey matter first formed in the spinal marrow correspond chiefly with the anterior columns. These are succeeded by lateral masses or columns, and somewhat later by small posterior columns. There are at first no commissures except by the passage of the deepest layer of cells across the middle line, but the fibres from the roots of the nerves when formed are traceable into the grey substance of their respective anterior and posterior columns.

The white substance is formed external to or on the surface of the deeper grey substance; but it is not yet determined whether it is wholly developed out of the cells composing the grey matter or from separate blastema to which the mesoblast may in part contribute. It is certainly combined with connective tissue elements, and its mode of formation is different from that of the grey substance, which is the more direct product of differentiation of the involuted epiblastic cells. How far the mesoblast takes part in the formation of the latter is still doubtful (see p. 192).

On the fifth and sixth days in the chick, according to Foster and Balfour, the white columns increase rapidly in size, and the anterior median fissure begins to be formed between the anterior columns by their swelling outwards and leaving its interval between them. It is at

first wide and shallow, and soon receives a lining of vascular connective tissue or pia mater. The commissures are now also formed; the anterior grey commissure first, then the posterior grey, and somewhat later the anterior white commissure.

Fig. 724.

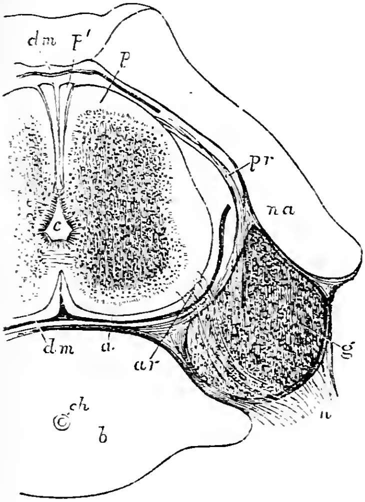


Fig. 724.—Transverse section of half the cartilaginous vertebral column and the spinal cord in the cervical part of a human embryo of from nine to ten weeks. (From Kölliker.) $\frac{10}{1}$

c, central canal lined with epithelium; *a*, anterior column; *p*, posterior column; *p'*, band of Goll; *g*, ganglion of the posterior root; *p r*, posterior root; *a r*, anterior root passing over the ganglion; *d m*, dura-matral sheath, omitted near *p r*, to show the posterior roots; *b*, body of the vertebra; *c h*, chorda dorsalis; *n a*, neural arch of the vertebra.

In the further increase of the anterior and lateral white columns as they thicken, they become more united together on each side, so that they can only be arbitrarily distinguished; the fibres of the roots of the nerves are traced through them into the grey matter; the cornua of grey matter become more and more developed, and the fissures between the white columns deepen, while the connective tissue or pia-matral septa run more completely inwards through the white substance.

Fig. 725.

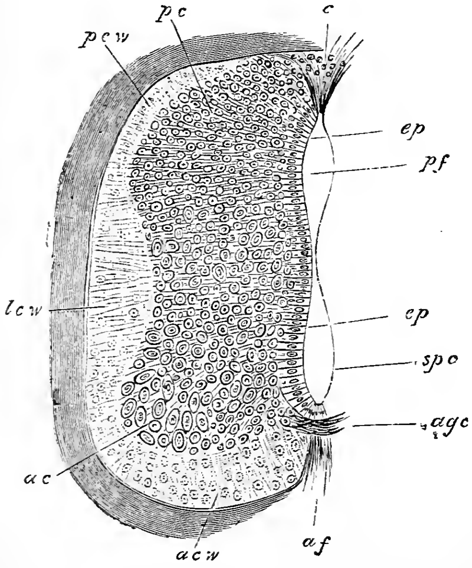


Fig. 725.—Transverse section of half of the spinal cord of the chick of seven days. (From Foster and Balfour.) Magnified.

pcw, posterior, *lcw*, lateral, and *acw*, anterior white columns; *pc*, posterior cornu of grey matter with small cells; *ac*, anterior grey cornu with large cells; *ep*, epithelium of the canal; *c*, the upper part now open and filled with tissue in the posterior fissure; *spc*, the lower division of the primitive medullary cavity, which remains as the permanent canal; *af*, anterior fissure left between the projecting anterior columns; *agc*, anterior grey commissure; *pf*, posterior fissure.

Angular cells with radiating processes make their appearance in the

grey matter, and the nerve-fibres both of the grey and white matter become more distinct.

The cylindrical cells lining the central canal retain their distinctness, and they are more completely separated from the grey matter by the delicate tissue of the ependyma. Throughout the greater part of the spinal cord the dorsal part of the primary medullary hollow is obliterated to form the fissure, but in the sacral region of birds it opens out in the rhomboidal sinus, and in the filum terminale of the human cord the whole primary medullary cavity remains.

The SPINAL CORD has been found by Kölliker already in the form of a cylinder in the cervical region of a human embryo of four weeks. Ununited borders have been seen by Tiedemann in the ninth week towards the lower end of the cord, the perfect closing of the furrow being delayed in that part, which is slightly enlarged, and presents a longitudinal median slit, analogous to the rhomboidal sinus in birds.

The *anterior fissure* of the cord is developed very early, and contains even from the first a process of the pia mater developed from mesoblast.

The *cervical* and *lumbar enlargements*, opposite the attachments of the brachial and crural nerves, appear at the end of the third month : in these situations the central canal, at that time not filled up, is somewhat larger than elsewhere (see figs. 733 and 736).

At first the cord occupies the whole length of the vertebral canal, so that there is no cauda equina. In the fourth month the vertebræ begin to grow more rapidly than the cord, so that the latter seems as it were to have been retracted within the canal, and the elongation of the roots of the nerves which gives rise to the *cauda equina* is commenced. At the ninth month, the lower end of the cord is opposite the third lumbar vertebra. (Kölliker, Lockhart Clarke, Bidder und Kupffer, Foster and Balfour.)

The origin of the roots of the spinal nerves will be referred to later.

THE BRAIN OR ENCEPHALON.

1. *General phenomena of development as ascertained in birds and mammals.*—Reference has previously been made to the simple form in which the brain at first presents itself in the anterior dilated portion of the primitive medullary tube, and its partial division into the three primary cerebral vesicles. These primary vesicles are named fore-brain, mid-brain, and hind-brain, and correspond most nearly to the regions of the third ventricle, the corpora quadrigemina and the medulla oblongata of the adult brain.

The changes which mainly tend to modify the form of this primitive brain are, 1st, the development on each side from the anterior vesicle of the primitive ocular vesicle; 2nd, the protrusion somewhat later from the forepart of the anterior cerebral vesicle of a bulging part, at first single or undivided, but which by a median cleft and lateral expansion becomes later the rudiment of the two cerebral hemispheres; and 3rd, the formation in the forepart of the posterior vesicle of a new encephalic rudiment corresponding to the cerebellum. Thus the first vesicle becomes converted into the cerebral hemispheres and vesicle of the third ventricle or thalamencephalon, the middle vesicle remains undivided, and the hinder vesicle becomes the cerebellum and medulla oblongata.

The formation of the primitive ocular vesicles, by an evolution of the lateral wall of the primitive medullary tube, gives to the first vesicle and the adjacent part of the head a much greater lateral width; but the cranial wall, though pushed out by the enlarging ocular vesicles, does

not follow closely the inflection of their surfaces. As the subsequent contraction of the stalk of the ocular vesicles progresses, these

Fig. 726.

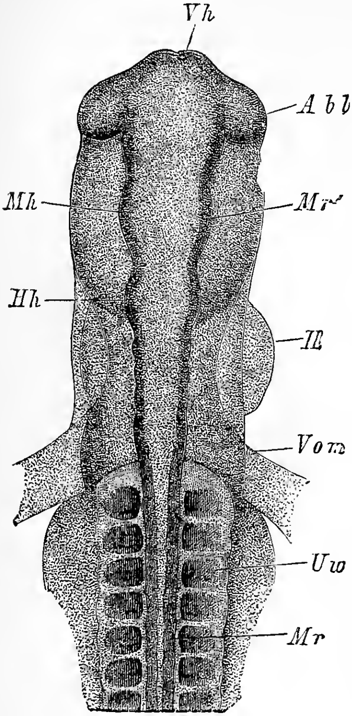


Fig. 726.—Fore-part of the embryo shown in fig. 689, viewed from the dorsal side. $\frac{30}{1}$. (From Kölliker.)

Vh, fore-brain ; *Abl*, ocular vesicles ; *Mh*, mid-brain ; *Hb*, hind-brain ; *H*, part of the heart seen bulging to the right side ; *Vom*, omphalo-mesenteric or vitelline veins entering the heart posteriorly ; *Mr*, medullary canal, spinal part ; *Mr'*, medullary wall of the mid-brain ; *Uw*, proto-vertebral somites.

vesicles are thrown more backwards and downwards by the development of the cerebral vesicles.

As the cerebral vesicles become enlarged, the cranial wall undergoes a corresponding expansion in the forepart of the head, the cavities of the lateral ventricles extend into their interior, and the vesicle of the thalamencephalon, which was at first the foremost part of the embryo-head, is thrown backwards into a somewhat deeper position.

The middle encephalic vesicle, increasing greatly in size, takes the most prominent part of the head superiorly, both from its own greater relative magnitude, and from the sudden bend which the head now takes below this vesicle in the great cranial flexure.

The formation of the cerebellum begins by a thickening in the upper

Fig. 727.

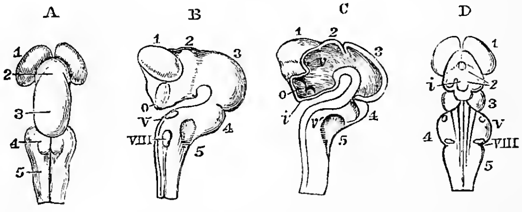


Fig. 727.—Four views of the brain of an embryo kitten in the stage of first division into the five cerebral rudiments, magnified three diameters. (From Reichert.)

A, from above ; B, from the side ; C, vertical section showing the interior ; D, from below.

1, Cerebral hemisphere, prosencephalon ; 2, thalamencephalon ; 3, mesencephalon, still single ; 4, cerebellum, epencephalon ; 5, myelencephalon, medulla oblongata ; *o*, optic nerves ; V, fifth pair ; VIII, eighth pair or glossopharyngeal and pneumogastric ; *i*, infundibulum ; *v*, *v'*, general ventricular cavity, opening at *v* into the lateral ventricle by the foramen of Monro.

and lateral walls of the part of the posterior primitive vesicle which is next to the mid-brain, and is accompanied by a deep inflection of the medullary tube between it and the remaining part of the vesicle which forms the medulla oblongata.

At the same time that these changes are progressing, two other remarkable phenomena occur, which, as presenting themselves very constantly in the brains of vertebrates, and having important morphological relations, may be mentioned at this place. These phenomena are both related to the thalamencephalon, and they consist, 1st, in the downward projection of a pointed funnel-shaped part of the cerebral wall, with a prolongation of the ventricular cavity within it, into the pituitary fossa,

Fig. 728.

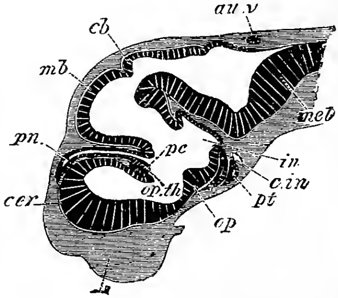


Fig. 728.—Longitudinal section through the brain of Scyllium canicula at an advanced stage of development. (From Balfour.)

cer, cerebral hemisphere ; *pn*, pineal gland ; *op.th*, optic thalamus ; *op*, optic chiasma ; *pt*, pituitary body ; *in*, infundibulum : *cb*, cerebellum ; *au.v*, recessus vestibuli, or passage from the auditory vesicle to the exterior ; *met*, medulla oblongata ; *c.in*, internal carotid artery.

preparatory to its union with the evoluted part of the mouth cavity by which the pituitary gland takes its rise ; and 2nd, in the thinning of the dorsal wall of the brain, and the prolongation of a part of that wall, which in the lower vertebrates reaches the cranial roof by a peculiar tubular extension, and is the homologue of the pineal gland.

There are thus distinguished the rudiments of five fundamental constituents of the brain, under which it will be found convenient to bring

Fig. 729.

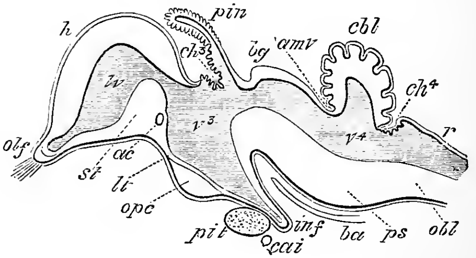


Fig. 729.—Outline of a longitudinal section through the brain of a chick of ten days. (After Mihalkovics.)

h, cerebral hemisphere ; *olf*, olfactory lobe and nerve ; *st*, corpus striatum ; *lv*, lateral ventricle ; *ac*, anterior commissure ; *lt*, lamina terminalis ; *opc*, optic commissure ; *pit*, pituitary gland ; *inf*, infundibulum ; *cai*, internal carotid artery ; v^3, third ventricle ; ch^3, choroid plexus of third ventricle ; *pin*, pineal gland ; *bg*, corpora bigemina ; *amv*, anterior medullary velum ; below which two last references are the aqueduct of Sylvius and crura cerebri ; *cbl*, cerebellum ; v^4, fourth ventricle ; *ba*, basilar artery ; *ps*, pons Varolii ; ch^4, choroid plexus of the fourth ventricle ; *obl*, medulla oblongata ; *r*, roof of fourth ventricle.

the notice of the development of the several parts forming the full-grown organ, and which may in this association be shortly enumerated as follows, viz. :—

1. The cerebral hemispheres, with their ventricular hollows or lateral

ventricles, the corpora striata, and the olfactory lobes,—a set of parts to which, as a whole, the name of *procerebrum* or *prosencephalon* may be given.

2. The *thalamencephalon* with its cavity or third ventricle, the primary ocular pedicles, and the infundibulum.

3. The *mesencephalon*, which is the same with the original middle vesicle, and comprises the corpora quadrigemina and crura cerebri with its contracted internal hollow, the iter a tertio ad quartum ventriculum of human anatomy.

4. The next part in succession is the *cerebellum*, along with which is included the pons Varolii and part of the fourth ventricle.

5. The hinder part, which passes into the spinal marrow, is the medulla oblongata, with the remainder of the fourth ventricle and its continuation into the central spinal canal.

Fig. 730.

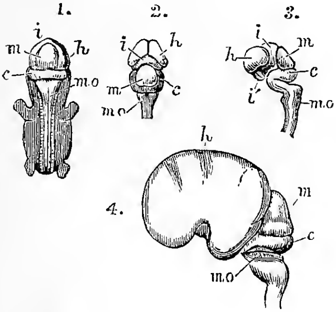


Fig. 730.—Sketches of the primitive parts of the human brain. (From Kölliker.)

1, 2, and 3 are from the human embryo of about seven weeks. 1, view of the whole embryo from behind, the brain and spinal cord exposed; 2, the posterior, and 3, the lateral view of the brain removed from the body; *h*, the cerebral hemisphere (prosencephalon); *i*, the thalamencephalon; *i'*, the infundibulum at the lower part of the same; *m*, the middle primary vesicle (mesencephalon); *c*, the cerebellum (epencephalon); *mo*, the medulla oblongata. Figure 3 shows also the several curves which take place in the development of the parts from the primitive medullary tube. In 4, a lateral view is given of the brain of a human embryo of three months: the enlargement of the cerebral hemisphere has covered in the optic thalami, leaving the tubercula quadrigemina, *m*, apparent.

In these five fundamental parts or rudiments of the brain, arising out of very simple modifications of the three primary encephalic vesicles, it is mainly by an increased thickening of the medullary wall in some of the parts, and the relative thinning, or even the entire removal of the substance in others, that the changes accompanying the formation of the cerebral masses are effected, while as a consequence of these and other modifications of form, the several parts of the internal cavity, or ventricles of the brain, acquire the different degrees of expansion and contraction, or the comparatively open or closed condition which they exhibit in after life. Thus the cerebral hemispheres and corpora striata are the main masses formed by the lateral thickening and expansion of the medullary walls of the procerebrum, while the corpus callosum and fornix are formed later by a deeper median development in connection with these parts: the thalami optici are the most solid parts of the lower and lateral region of the second rudiment: the corpora quadrigemina are thickenings of the upper wall of the third rudiment, while the crura cerebri arise by increased deposit in its lower part; the cerebellum may be regarded as a large deposit in the upper wall of the fourth rudiment, while the pons Varolii is a thickening of its lower wall; and the parts composing the medulla oblongata are principally formed by increased deposit in the lower and lateral wall of the fifth rudiment.

Thus, also, the lateral ventricles are two expansions of the forepart of the original ventricular cavity which result from the dilatation of the vesicles of the right and left cerebral hemispheres, and communicate with the central or third ventricle by the common foramen of Monro. The central or third ventricle, originally the foremost part of the medullary hollow, is narrowed on the sides by the increased development

Fig. 731.

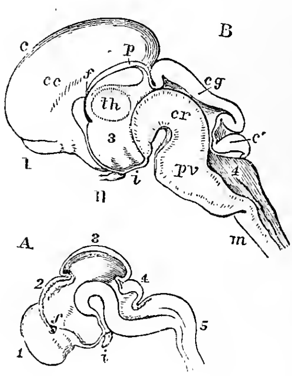


Fig. 731.—Vertical sections of embryonic brains in two stages of transition from the rudimentary condition, magnified three diameters. (From Reichert.)

A, Brain of the embryo pig in commencing state of transition. 1, Right cerebral hemisphere; 2, thalamencephalon and position of the pineal gland; 3, mid-brain, with a large cavity; *f*, foramen of Monro; *i*, infundibulum; 4, cerebellum; 5, medulla oblongata.

B, Brain of the embryo of the cat, more advanced. *c*, Cerebral hemisphere passing backwards so as to cover the other parts; I, olfactory bulb; II, optic nerve; *th*, thalamus opticus; *f*, foramen of Monro; *cc*, corpus callosum; *p*, pineal gland; *i*, infundibulum; *cg*, corpora quadrigemina, not yet divided; 3, third ventricle; *cr*, crura cerebri, below the aqueduct of Sylvius, now reduced in width; *c'*, cerebellum; 4, fourth ventricle; *pv*, Pons Varolii; *m*, medulla oblongata.

of the thalami optici, while inferiorly it is prolonged and projects downwards as infundibulum into the pituitary fossa; and on the upper side the wall of this ventricle comes to be opened up by the thinning away of its medullary substance, and otherwise modified in connection with the formation of the pineal gland. The continuation backwards of the original ventricular hollow, greatly narrowed by the ultimate thickening of the substance of the corpora quadrigemina and crura cerebri, forms the aqueduct of Sylvius, and is succeeded by the more expanded cavity

Fig. 732.

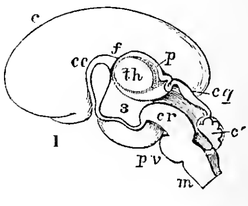


Fig. 732.—Vertical section of the brain of a human embryo of fourteen weeks, magnified three diameters. (From Reichert.)

c, cerebral hemisphere; *cc*, corpus callosum beginning to pass back, *f*, foramen of Monro; *p*, membrane over the third ventricle and the pineal gland; *th*, thalamus opticus; 3, third ventricle; I, olfactory bulb; *cq*, corpora quadrigemina, mesencephalon; *cr*, crura cerebri, and above them the aqueduct of Sylvius still wide; *c'*, cerebellum, and below it the fourth ventricle; *pv*, Pons Varolii; *m*, medulla oblongata.

of the fourth ventricle, lying between the cerebellum and the lower wall. The upper wall of the latter cavity undergoes great thinning like that of the third ventricle, so as to be reduced in the part before the cerebellum to the thin lamina forming the valve of Vieussens, and in the part behind it to be covered only by membrane, and to present an opening from the cavity into the posterior sub-arachnoid space.

From what has before been said of the relation of the fundamental parts of the brain to the basis of the skull, it will be seen that the cere-

bral development is intimately connected also with the great cranial flexure which occurs at the pituitary fossa; for while the infundibular prolongation of the thalamencephalon projects down into this fossa, and the lamina terminalis lies in front in the position of the original foremost part of the encephalon, certain parts of the brain may be considered as situated posterior to this point, viz., the mesencephalon with crura cerebri, cerebellum with pons Varolii, and medulla oblongata, while the cerebral hemispheres, with the corpora striata, corpus callosum, and fornix, may be considered as formed in their earlier condition by forward expansion, and as situated in front of this turning point. But though the connections of the cerebral hemispheres with the rest of the brain may thus be regarded as anterior to the cranial centre, and while in their earlier stages, and still of small size, they are actually placed as in the lowest vertebrates entirely in front of it, yet by the later great proportional development in the higher animals, and especially in man, the cerebral hemispheres come to progress backwards, and successively to cover superiorly the thalami, corpora quadrigemina, the cerebellum, and the medulla oblongata.

The developmental relation of the several parts of the brain to its fundamental rudiments may be stated in the following tabular form :

I. Anterior primary Vesicle,	1. Prosencephalon.* Fore-brain.	Cerebral Hemispheres, Corpora Striata, Corpus Callosum, Fornix, Lateral Ventricles, Olfactory bulb (Rhinencephalon).
	2. Thalamencephalon. (Diencephalon.) Inter-brain.	Thalami Optici, Pineal gland, Pituitary body, Third Ventricle, Optic nerve (primarily).
II. Middle primary Vesicle,	3. Mesencephalon. Mid-brain.	Corpora Quadrigemina, Crura Cerebri, Aqueduct of Sylvius, Optic nerve (secondarily).
III. Posterior primary Vesicle.	4. Epencephalon. Hind-brain.	Cerebellum, Pons Varolii, anterior part of the Fourth Ventricle.
	5. Metencephalon. After-brain.	Medulla Oblongata, Fourth Ventricle, Auditory nerve.

(See the reference to works on the development of the brain under the Nos. 184—194.)

FARTHER DEVELOPMENT OF THE BRAIN IN MAN AND MAMMALS.

The full history of the development of the brain is so extensive and complicated a subject that it will be necessary to limit ourselves here to a very brief indication of the principal facts regarding it, proceeding from behind forwards in the order of the five fundamental parts of the brain above-mentioned.

1. Medulla Oblongata, Metencephalon, After-brain.—The medullary roof of this part becomes at an early period more and more widened out laterally, and reduced in thickness till at last scarcely any nervous substance remains, and the lateral parts, along with the inferior, thickening by the great increase of the medullary tissue, are thrown towards the side, and thus give rise to the wide space which forms the fourth ventricle, bounded posteriorly by the narrowing calamus scriptorius, and leading at its point into the canal of the spinal marrow. There is subsequently formed in the roof the opening which leads from the fourth ventricle into the subarachnoid space, and the pia mater, rich in blood-vessels, becomes folded over the roof and forms the plexus known as the choroid of the fourth ventricle.

The three more solid constituent parts of the medulla oblongata begin to be

* This and the four following terms are adopted as applicable to the principal secondary divisions of the primary medullary tube, and as corresponding to the commonly received names of the German embryologists, viz., Vorderhirn, Zwischenhirn, Mittelhirn, Hinterhirn, and Nachhirn, or their less used English translations, given above.

distinguishable about the third month; first the *restiform* bodies, which are connected with the commencing cerebellum, and afterwards the anterior pyramids and olives. The *anterior pyramids* become prominent on the surface and distinctly defined in the fifth month; and by this time also their decussation is evident. The *olivary* fasciculi are early distinguishable, but the proper *olivary body*, or tubercle, does not appear till about the sixth month. The *fasciolæ cinereæ* of the fourth ventricle can be seen at the fourth or fifth month, but the *white striæ* not until after birth.

2. The Cerebellum, Epencephalon, Hind-brain.—In the human embryo the cerebellum exists at the end of the second month, as a thin medullary lamina, forming, as in many of the lower vertebrate animals, an arch behind the corpora quadrigemina across the wide primitive medullary tube.

According to Bischoff, the cerebellum does not commence, as was previously supposed, by two lateral plates which grow up and meet each other in the middle line; but a continuous deposit of nervous substance takes place across this part

Fig. 733.

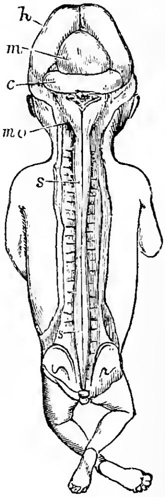


Fig. 733.—Brain and spinal cord exposed from behind in a fœtus of three months. (From Kölliker.)

h, the hemispheres; *m*, the mesencephalic vesicle or corpora quadrigemina, *c*, the cerebellum; below this are the medulla oblongata, *mo*, and fourth ventricle, with remains of the membrana obturatoria. The spinal cord, *s*, extends to the lower end of the sacral canal, and presents the brachial and crural enlargements.

of the medullary tube, and closes it in at once. This layer of nervous matter, which is soon connected with the corpora restiformia, or inferior peduncles, increases gradually up to the fourth month. The middle lobe is the first formed, and remains for a considerable time the principal mass of the cerebellum. The lateral lobes follow, and there is seen about the fifth month a division of these into the subordinate lobes; at the sixth, these lobes send out *folia*, which are at first simple, but afterwards become subdivided. Moreover, the *hemispheres* of the cerebellum are now relatively larger than its median portion, or *worm*. In the seventh month the organ is more complete, and the *flocculus* and *posterior velum*, with the other parts of the inferior vermiform process, are now distinguishable, except the *amygdalæ*, which are later in appearing.

Of the *peduncles* of the cerebellum, the *inferior* pair (corpora restiformia) are the first seen—viz., about the third month; the *middle* peduncles are perceptible in the fourth month; and at the fifth, the *superior* peduncles and the Vieussenian valve. The *pons Varolii* is formed, as it were, by the fibres from the hemispheres of the cerebellum embracing the pyramidal and olivary fasciculi of the medulla oblongata below. According to V. Baer, the bend which takes place at this part of the encephalon thrusts down a mass of nervous substance before any fibres can be seen; and in this substance transverse fibres, continuous with those of the cerebellum, are afterwards developed. From its relation to the cerebellar hemispheres the pons keeps pace with them in its growth; and, in conformity with this relation, its transverse fibres are few, or entirely wanting in those animals in which there is a corresponding deficiency or absence of the lateral parts of the cerebellum, as in marsupials and monotremes.

3. The Mesencephalon, Mid-brain.—The *corpora quadrigemina* are formed in the upper part of the middle cephalic vesicle; the hollow in the interior of which communicates with those of the first and third vesicles. The corpora quadrigemina, in the early condition of the human embryo, are of great proportionate volume, in harmony with what is seen in the lower vertebrata; but subsequently they do not grow so fast as the anterior parts of the encephalon, and are therefore soon overlaid by the cerebral hemispheres, which at the sixth month

cover them completely. Moreover, they become gradually solid by the deposition of matter within them; and as, in the meantime, the *cerebral peduncles* are increasing rapidly in size in the floor of this middle cephalic vesicle, the cavity in its interior is quickly filled up, with the exception of the narrow passage named the *Sylvian aqueduct*. The fillet is distinguishable in the fourth month. The corpora quadrigemina of the two sides are not marked off from each other by a vertical median groove until about the sixth month; and the transverse depression separating the anterior and posterior pairs is first seen about the seventh month of intra-uterine life.

Fig. 734.

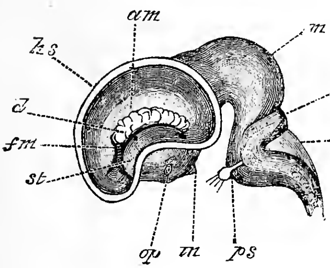


Fig. 734.—Lateral view of the brain of an embryo calf of 5 cm. (From Balfour, after Mihalkovics.)

The outer wall of the left hemisphere is removed to show the interior of the lateral ventricle; *hs*, cut wall of the hemisphere; *st*, corpus striatum; *am*, hippocampus major; *d*, choroid plexus of ventricle; *fm*, foramen of Monro; *op*, optic tract; *in*, infundibulum; *mb*, midbrain; *cb*, cerebellum; IV.V, roof of fourth ventricle; *ps*, pons Varolii; with fifth nerve and Gasserian ganglion.

The internal geniculate bodies belong to this division of the brain.

4. The Thalamencephalon, Inter-brain.—It is from this part, constituting at first the whole and subsequently the hinder part of the anterior primary encephalic vesicle, that the optic vesicles are developed in the earliest period, and the forepart is that in connection with which the cerebral hemispheres and accompanying parts are formed. The thalamus opticus of each side is formed by a lateral thickening of the medullary wall, while the interval between, descending towards the base, constitutes the cavity of the third ventricle with its prolongation in the infundibulum. The grey commissure afterwards stretches across the ventricular

Fig. 735.

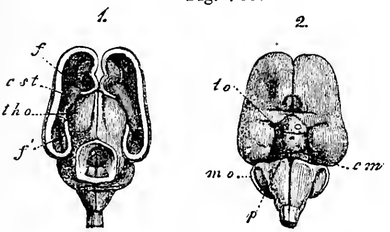


Fig. 735.—Brain of the human embryo of three months. Natural size. (From Kölliker.)

In 1 the view is from above, the upper part of the cerebral hemispheres and mesencephalon having been removed. *f*, fore part of the divided wall of the hemisphere; *f'*, hind part of the same which becomes the hippocampus turned in; *cst*, corpus striatum; *tho*, thalamus opticus.

In 2 the lower surface is represented; *to*, tractus opticus; and in front of this the olfactory bulbs and tracts; *cm*, single mass of the corpora mammillaria not yet divided; *p*, pons Varolii. The cerebellum and medulla oblongata, *mo*, are seen behind and to the sides in both figures.

cavity. The medullary roof of this part on the other hand thins down rapidly, and is at last reduced only to a folded membrane, in connection with the pia mater of which the choroid plexus of the third ventricle is formed. The hinder part of the roof is developed by a peculiar process to be noticed later into the pineal gland, which remains united on each side by its pedicles to the thalamus, and behind these a transverse band is formed as posterior commissure.

The lamina terminalis (lamina cinerea) continues to close the third ventricle in front, below it the optic commissure forms the floor of the ventricle, and

further back the infundibulum descends to be united in the sella turcica with the tissue adjoining the posterior lobe of the pituitary body.

The two *optic thalami*, formed from the posterior and outer part of the anterior vesicle, consist at first of a single hollow sac of nervous matter, the cavity of which communicates on each side in front with that of the commencing cerebral hemispheres, and behind with that of the middle cephalic vesicle (corpora quadrigemina). Soon, however, by increased deposit taking place in their interior behind, below, and at the sides, the thalami become solid, and at the same time a cleft or fissure appears between them above, and penetrates down to the internal cavity, which continues open at the back part opposite the entrance of the Sylvian aqueduct. This cleft or fissure is the *third ventricle*. Behind, the two thalami continue united by the *posterior commissure*, which is distinguishable about the end of the third month, and also by the *peduncles of the pineal gland*. The *soft commissure* probably exists from an early period, although it could not be detected by Tiedemann until the ninth month.

Fig. 736.

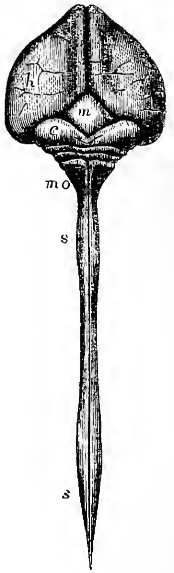


Fig. 736.—Brain and spinal cord of a fœtus of four months, seen from behind. (From Kölliker.)

h, hemispheres of the cerebrum; *m*, corpora quadrigemina or mesencephalon; *c*, cerebellum; *mo*, medulla oblongata, the fourth ventricle being overlapped by the cerebellum; *s s*, the spinal cord with its brachial and crural enlargements.

At an early period the *optic tracts* may be recognised as hollow prolongations from the outer part of the wall of the thalami while they are still vesicular. At the fourth month these tracts are distinctly formed. They subsequently are prolonged backwards into connection with the corpora quadrigemina.

The formation of the pineal gland and pituitary body presents some of the most interesting phenomena which are connected with the development of the thalamencephalon.

Pineal Gland. Epiphysis Cerebri.—As already stated, this body is formed by an out-folding from the back part of the inter-brain roof, at a place where the opposite sides remain united by nervous matter afterwards giving rise to the pineal peduncles. This body consists at first in all vertebrates of medullary substance covered by pia mater, and forms a median projection upwards, which in the lower tribes is also directed forwards in the form of a tube which reaches the roof of the cranium, and in some is united with or even passes through the cranial wall. It is in all deeply indented by vascular folds and growths of the pia mater. In mammals the original development of the pineal gland is the same as in the lower tribes; but it remains comparatively short, and its direction is backwards; and though it is at first permeated by epithelial tubes, or subdivisions of the ventricular cavity, it becomes at a later period solid by the deposit of various cellular and other materials. The gritty deposit was found in it by Sœmmerring at birth.

Pituitary body. Hypophysis Cerebri.—The general nature of this body in connection with an outgrowth of the brain on the one hand and a diverticulum of the alimentary canal on the other, and which was first pointed out by Rathke (1838, No. 195), has been already adverted to. The researches of W. Müller (No. 197), Goette (No. 200), and Mihalkovics (No. 198), have fully confirmed Rathke's view, and lead to the following general conclusions regarding it.

The infundibulum, as is well known, is a prolongation of the medullary wall of the third ventricle, originally in continuity with the epiblast; while the diverticulum from the alimentary canal is not, as was at one time supposed, from the pharynx, but from the mouth, and its lining is therefore continuous with the same layer of the blastoderm. This diverticulum is formed at an early period from

the middle of the upper and back part of the buccal cavity before the faucial opening into the pharynx has taken place. The anterior attenuated extremity of the notochord is placed between the cerebral and buccal outgrowths, but it disappears as the lower one extends upwards and comes to unite with the infundibulum, and then the notochord is lost in the floor of the pituitary fossa with which both the outgrowths cohere (Mihalkovics)

Fig. 737.

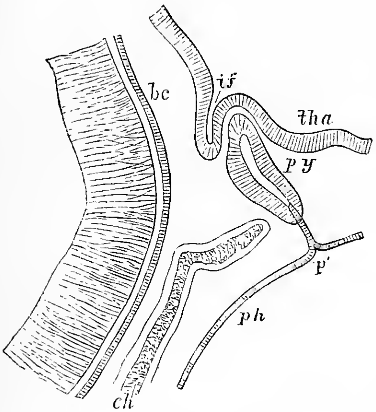


Fig. 737.—Vertical section of the infundibulum and pituitary diverticulum in the rabbit's embryo, after the opening of the fauces. (From Mihalkovics.)

For the earlier stages see fig. 705, p. 807, A and B. *bc*, dorsum sellæ; *if*, infundibulum; *tha*, floor of thalamencephalon; *py*, pituitary diverticulum, now closed; *p'*, stalk of original communication with the mouth; *ph*, pharynx; *ch*, notochord in the spheno-occipital part of the cranial basis.

The flask-like outgrowth of the buccal epiblast which gives rise to the hypophysis cerebri, is now gradually shut off from the corneous layer and cavity of the mouth by the constriction and subsequent closure of its communicating pedicle. There remains, however, for a considerable time, a longish thread of union between the two. The epithelium of the enclosed portion subsequently undergoes development into glandular cæca and cell-cords, and its internal cavity becomes gradually obliterated. This forms the anterior part or lobe of the pituitary body. The posterior part owes its origin in all vertebrates to the combination with mesoblastic tissue of a widened extension of the infundibular process of the brain, which is thrust in between the sac of the pituitary body and the dorsum sellæ. The nervous structure of this posterior lobe afterwards disappears in the higher animals, but in the lower the posterior lobe retains its place as a part of the brain.

The possibility of establishing a general homology between vertebrate and invertebrate animals, involves important considerations as to the relations of the forepart of the alimentary canal to the brain. In a recent memoir on this subject (No. 201), Professor Owen puts forward the view that the "conario-hypophysial tract," or passage through the pituitary diverticulum, infundibulum, third ventricle and pineal gland, may have been the means of carrying the anterior part of the alimentary canal from the ventral or hæmal to the dorsal or neural side of the head in an ancestral form of the vertebrate animal, and that thus (one of them being inverted) the several sets of organs in the two great divisions of the animal kingdom might be brought into corresponding relative position. According to the view taken by Dohrn (No. 199), the fourth ventricle is the place where the œsophagus may be supposed to have pierced the nervous ring.

5. Prosencephalon, Fore-brain.—Each *hemisphere-vesicle* may be considered to consist of two parts: one of these is the part which from the interior appears as the corpus striatum, and from the exterior as the island of Reil, or central lobe: the other forms the expanded or covering portion of the hemisphere, and is designated by Reichert the *mantle*. The lateral ventricles are placed internally between these parts. The aperture existing at the constricted neck of the ventricle where it expands into the hemispheres is the foramen of Monro.

The *corpora striata*, it will be observed, have a different origin from the optic thalami; for, while the latter are formed by thickening of the circumferential wall of a part of the first cerebral vesicle, and thus correspond in their origin with the parts of the encephalon behind them, the corpora striata appear as

thickenings of the floor of the hemisphere-vesicles, which are lateral off-shoots from the original medullary tube. On this account, Reichert considers the brain primarily divisible into the stem, which comprises the whole encephalon forwards to the tænia semicircularis, and the hemisphere-vesicles, which include the corpora striata and hemispheres.

The cerebral hemispheres undergo enlargement at an early period in mammals,

Fig. 738.

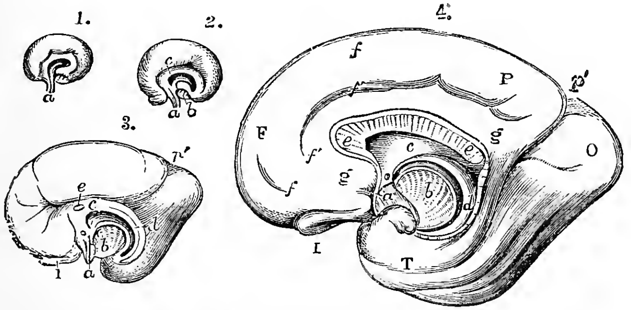


Fig. 738.—Semidiagrammatic views of the inner surface of the right cerebral hemisphere of the fœtal brain at various stages of development. (From Schmidt.)

1, 2, and 3, are from fœtuses of the respective ages of eight, ten, and sixteen weeks; 4, from a fœtus of six months. *a*, lamina terminalis or part of the first primary vesicle which adheres to the sella turcica; *b*, section of the cerebral peduncle as it passes into the thalamus and corpus striatum; the arched line which surrounds this bounds the great cerebral fissure; *c*, anterior part of the fornix and the septum lucidum; *d*, inner part of the arch of the cerebrum, afterwards the hippocampus major and posterior part of the fornix; *e*, corpus callosum very short in 3, elongated backwards in 4; in 4, *f*, the marginal convolution; *f'*, calloso-marginal fissure; *g*, gyrus fornicatus; *p'*, the parieto-occipital fissure descending to meet the calcarine fissure; I, olfactory bulb; F, P, O, T, frontal, parietal, occipital and temporal lobes.

and especially in the human embryo, so that at the tenth week they have greatly surpassed in size all the other parts of the brain. They then form large hollow bodies with comparatively thin walls superiorly, the lateral ventricles being greatly

Fig. 739.

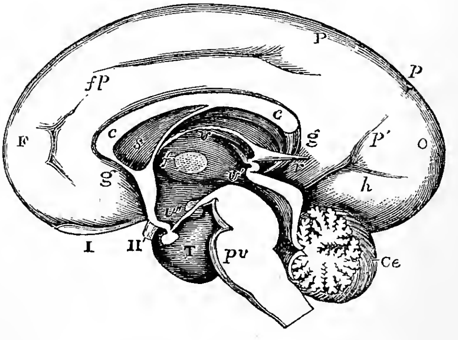


Fig. 739.—View of the inner surface of the right half of the fœtal brain of about six months. (From Reichert.)

F, frontal lobe; P, parietal; O, occipital; T, temporal; I, olfactory bulb; II, right optic nerve; *fp*, calloso-marginal fissure; *p*, external; *p'*, internal parts of the parieto-occipital fissure; *h*, calcarine fissure; *g*, gyrus fornicatus; *c*, *c*, corpus callosum; *s*, septum lucidum; *f*, placed between the middle commissure and the foramen of Monro; *v*, in the upper part of the third ventricle immediately below the velum interpositum and fornix; *v'*, in the back part of the third ventricle below the pineal gland, and pointing by a line to the aqueduct of Sylvius; *v''*, in the lower part of the third ventricle above the infundibulum; *r*, recessus pinealis passing backwards from the tela choroidea; *pv*, pons Varolii; *Ce*, cerebellum.

dilated, and communicating by a wide aperture with each other, and with the third ventricle, by the foramen of Monro. The growth of the hemispheres takes place progressively from before backwards, so that they come to cover in succession the thalami, corpora quadrigemina and cerebellum, which all originally stood in a series behind them, as they do permanently in the lowest vertebrates. By the end of the third month the hemispheres have extended so far backwards as to cover the thalami; at the fourth they reach the corpora quadrigemina; at the sixth they cover those bodies and great part of the cerebellum, beyond which they project still further backwards by the end of the seventh month.

The floor especially of the hemispheres thickens considerably, and the corpus striatum increasing greatly in magnitude, at the same time projects upwards into the lateral ventricles so as to give these cavities an arched form and mark out their anterior and descending cornua, while externally the distinction between the frontal and temporal lobes is indicated by the wide depression of the fossa of Sylvius. The floor of this part below the corpora striata becomes the island of Reil, or central lobe. The corpora striata and thalami, which are at first distinct, become more and more completely united together.

Fig. 740.

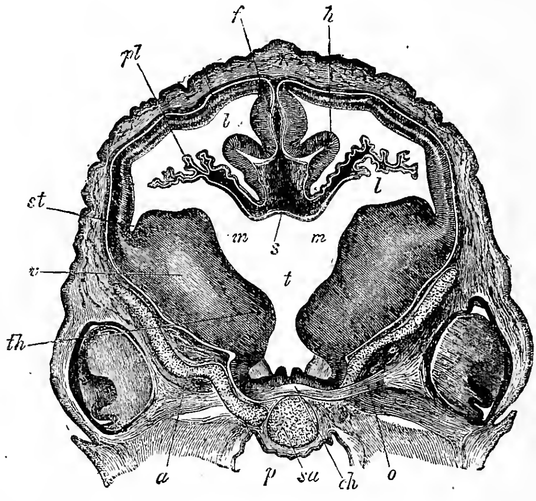


Fig. 740.—TRANSVERSE SECTION THROUGH THE BRAIN OF A SHEEP'S EMBRYO OF 2·7 CM. IN LENGTH. (From Balfour, after Kölliker.)

The section passes through the hemispheres and third ventricle. *st*, corpus striatum; *th*, optic thalamus; *t*, third ventricle; *c'*, their divergence into the walls of the hemispheres; *l*, lateral ventricle with choroid plexus *pl*; *h*, hippocampus major; *f*, primitive falx; *a*, orbito-sphenoid; *sa*, presphenoid; *p*, pharynx; *ch*, chiasma; *o*, optic nerve; *mm*, foramen of Monro; *s*, covering of lateral ventricles.

A deep notch separates the hemispheres above and posteriorly, but in front they are united together in the place of the original lamina terminalis, and here as farther back the inner walls becoming thinner are united together in a narrow partition which is the source of the septum lucidum and the commissures. The first of these to arise is the anterior commissure, which is also the lowest and unites the corpora striata. The fornix comes next in its anterior part, which with its pillars and the corpora albicantia is at first single and median; the posterior pillars follow, running back on each side into the cornu Ammonis of the descending cornua. The corpus callosum is last formed, consisting at first only of its fore part, as is permanently the case in monotremes and marsupials; but as the hemispheres extend themselves backwards, the corpus callosum elongates

in the same direction, thus forming a roof for the subjacent lateral ventricles and other parts.

The fifth ventricle in the septum lucidum is not a part of the original common ventricular cavity of the brain, but is formed separately.

At the lower part of the inner walls two horizontal folds make their appearance below those of the fornix and hippocampi, which are covered by pia mater, and which, extending backwards from the foramen of Monro, cover in the third ventricle and occupy the great transverse fissure of the brain. These folds, extending themselves laterally and backwards, and becoming more and more plicated and vascular at the edges, give rise to the choroid plexus of the lateral ventricles and the velum interpositum.

The *olfactory lobes* are outgrowths from the lower and lateral parts of the cerebral hemispheres, being more immediately connected with the frontal lobes, but extending through the fissure of Sylvius as far as the temporal or middle lobes. They are at first hollow, and in some animals their cavity is in permanent communication with the lateral ventricles. In man they become solid at an early period.

Development of the Convolutions and Sulci.—Adopting the distinction of the convolutions and sulci of the cerebral hemispheres as of two kinds, viz., "primitive" and "secondary," according as the former result from a folding of

Fig. 741.

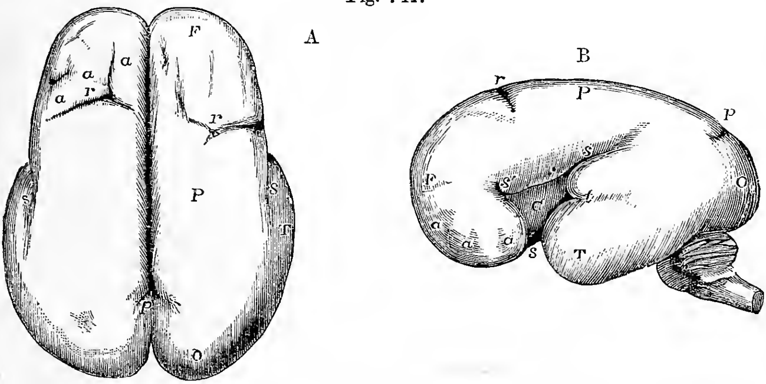


Fig. 741.—The Surface of the Fœtal Brain at Six Months. (From R. Wagner.)

This figure is intended to show the commencement of the formation of the principal fissures and convolutions. A, from above; B, from the left side. F, frontal lobe; P, parietal; O, occipital; T, temporal; *a*, *a*, *a*, slight appearance of the several frontal convolutions; *s*, the Sylvian fissure; *s'*, its anterior division; within it, C, the central lobe or convolutions of the island; *r*, fissure of Rolando; *p*, the parieto-occipital fissure.

the whole substance of the wall of the hemisphere, while the latter consist merely of depressions and elevations of its more superficial portion, it may be stated, with respect to their development, that the first of the primitive sulci to appear is the fissure of Sylvius, which is visible before the end of the third month (Ecker) as a wide shallow depression or fossa between the anterior and middle lobe of each hemisphere. Of the remaining primitive sulci, the hippocampal or dentate, the parieto-occipital and the calcarine, also begin to appear during the third month, and by the end of the fifth month are well established.

The secondary sulci begin to appear about the fifth or sixth month; the first of these to be seen is the sulcus centralis, or fissure of Rolando. By the end of the sixth month the transverse frontal and inferior frontal furrows have appeared on the otherwise smooth surface of the frontal lobe, and at about the same time the first indications of the intraparietal fissure, with its continuation on the occipital lobe as the superior occipital furrow, the parallel, the calloso-marginal

and collateral fissures become visible on the outer and inner aspects of the hemispheres. The lower surface now shows a slight trace of the inferior temporal furrow; and the fissure of Sylvius, which was at first a wide fossa, at this period begins to close in, especially at its hinder portion, an indication of its anterior division becoming now visible.

By the end of the seventh month nearly all the chief features of the cerebral convolutions and sulci have appeared. The superior frontal fissure can now be seen, and the three frontal convolutions are well marked. The fissure of Rolando has increased in length and depth. While the sulci that have already been spoken of are becoming better marked, the transverse occipital appears for the first time. Within the fissure of Sylvius, which has now a triangular form, two depressions are seen, the anterior bounding a prolongation of the olfactory tract, the posterior dividing the greater portion of the floor of the fissure into a fore and hind part. The island of Reil shows three convolutions divided by the forked sulcus insulæ primus. The sulci visible on the under surface of the hemispheres are still few and indistinct. Indications are found of a branched orbital sulcus, and of the olfactory sulcus, in which lie the olfactory bulb and tract. The middle temporal convolution, and the uncus and gyrus hippocampi, have now become fairly prominent.

During the eighth month a furrow appears behind the fissure of Rolando, parallel to it, and joining the intraparietal. This is the sulcus postcentralis of Ecker. The transverse occipital furrow now becomes very distinct, and joins the intraparietal farther back. The last fissures to appear are the inferior occipito-temporal and a small furrow crossing the end of the calloso-marginal. (Consult Nos. 28, 190, and 191.).

II. THE NERVES.

Very little was known till lately of the exact mode of origin of the peripheral nerves, and it was generally supposed that they were formed,

Fig. 742.

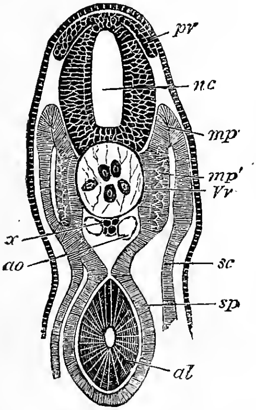


Fig. 742.—Transverse section through the trunk of an embryo shark, to show the neural crest. (From Balfour.)

nc, neural canal; *pr*, posterior root of spinal nerve; *x*, sub-notochordal rod; *ao*, aorta; *sc*, parietal mesoblast; *sp*, visceral mesoblast; *mp'*, muscle plate; *mp*, portion of muscle plate converted into muscle; *Vv*, portion of the vertebral plate which will give rise to the vertebral bodies; *al*, alimentary canal.

as held by Remak, in more or less immediate connection with the parts of mesoblastic origin in which they were distributed. The only known fact inconsistent with this view was that the anterior or motor roots of the spinal nerves had been found to bud out from the ventral side of the spinal cord. The recent researches especially of His, Balfour, and Marshall, Kölliker, Hensen and others, have thrown quite a new light on this subject, and have shown that all the peripheral nerves, cerebro-spinal and sympathetic, with their ganglia, emanate originally from the primary brain and spinal marrow, that they have therefore an epiblastic origin, and that they spread more or less from thence into the different parts of the body. (See Nos. 28 and 202—205.)

Spinal Nerves.—Following the description of their origin given by Balfour and Marshall, it may be stated that the posterior roots of the spinal nerves and most of the cranial nerves, with their respective ganglia, which

are formed before the anterior roots, proceed from a series of cellular swellings, constituting the *neural crest*, which are in continuity with the medullary plates close to the place of inflection of the epiblast into the involution which forms the primary brain and spinal cord. These root swellings are in some animals connected together by a longitudinal band or commissure. In the primitive projections there are soon distinguished a narrower first part or root, then a thicker part, the ganglion, and further down a part of the nerve extending beyond it. The root originally connected with the upper part of the medullary wall close to the median line slips down, as it were, upon the side, and is subsequently

Fig. 743.

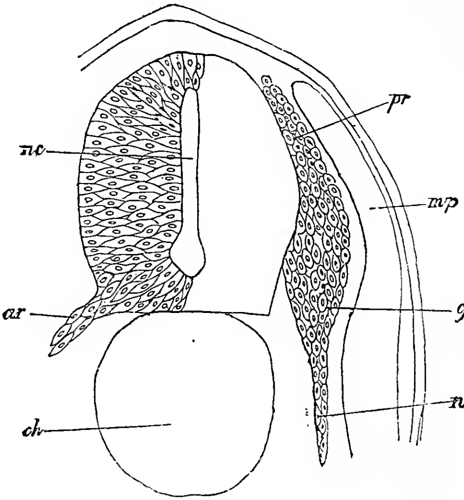


Fig. 743.—Section through the dorsal part of the trunk of a Torpedo embryo. (From Balfour.)

pr, posterior root of spinal nerve; *g*, spinal ganglion; *n*, nerve; *ar*, anterior root; *ch*, notochord; *nc*, neural canal; *mp*, muscle-plate.

united laterally with the medullary wall at a lower place, leaving the upper end of the root for a time apparently free. This process begins in the chick at the end of the second day, and in the embryo of the rabbit on the ninth day.

The anterior roots of the spinal nerves are also outgrowths from the medullary wall. They begin to appear somewhat later than the posterior roots, as projections from its ventral side, and extending from thence outwards, come to join the nerve which emanates from the ganglion of the posterior root; and from this point the compound nerve grows towards the periphery or region of its distribution. The place at which the anterior roots spring from the spinal cord is not opposite to the corresponding posterior root, but midway between that root and the succeeding one. Both roots and ganglion have at first a cellular structure, and their fibres are of later origin, the cells being largest in the ganglion, and the fibres appearing earlier in the anterior than in the posterior roots.

Cranial Nerves.—Most of the cranial nerves, viz., the olfactory, the 3rd, 5th, and 7th, the auditory, the glossopharyngeal, and the vagus, arise from a neural crest in a manner analogous to the spinal posterior roots; and in the chick the ridge from which some of them spring is perceptible even before the closure of the medullary canal at its dorsal lip of inflection (Marshall); and as it is more immediately attached to the medullary than to the epidermal part of the epiblast, the cranial nerve-roots may be regarded as taking their origin from the rudimentary brain.

The cerebral neural crest is continuous with that of the spinal

marrow. It extends to the roof of the mid-brain, and there is the same shifting downwards of the attachment of the roots to the neural crest as in the spinal nerves. In most of the nerves it has been observed that a subdivision occurs into portions representing a root, a ganglion, and a peripheral nerve-trunk. The change of the place of attachment is most remarkable in the case of the third nerve, which is carried down quite to the lower surface of the mid-brain.

The sixth and the twelfth (or hypoglossal) nerves may arise, according to Marshall, as motor or lower roots of certain of the other nerves; but

Fig. 744.

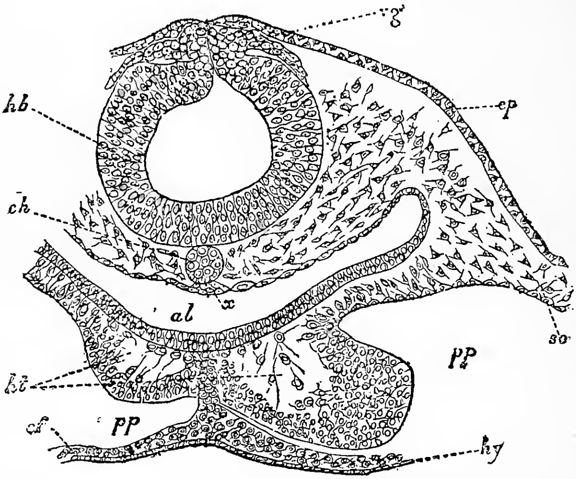


Fig. 744.—Transverse section through the posterior part of the head of an embryo chick of 30 hours. (From Balfour.)

hb, hind-brain; *vg*, vagus nerve; *ep*, epiblast; *ch*, notochord; *x*, sub-notochordal rod; *al*, throat; *ht*, heart; *pp*, body-cavity; *so*, parietal mesoblast; *sf*, visceral mesoblast; *hy*, hypoblast.

the mode of origin of these two nerves, as well as of the fourth, has not yet been fully ascertained, and Balfour doubts whether the cranial nerves before described as arising dorsally from a neural ridge or crest, are, like the dorsal roots of the spinal nerves, exclusively sensory. Some of them, he holds, are undoubtedly mixed, and all of them may be so. (No. 205.)

The olfactory nerve is certainly an outgrowth from the fore-brain; but whether from an extension forwards of the neural crest or not is still doubtful. In the olfactory nerve of mammalian embryoes, A. Fraser has observed the root ganglion and two main divisions of the nerve forking over the nasal pit (see fig. 745).

The origin of the Optic nerve and retina from the primitive medullary fore-brain (as will be shown later) is different from that of all other nerves.

The fifth nerve, shortly after its origin in connection with a neural crest like the rest, undergoes the shifting change of position, and is united to the rudiment of the large Gasserian ganglion. Of its three principal branches the inferior maxillary belongs to the mandibular arch, in the hinder part of which it is placed. Its ophthalmic and superior maxillary divisions are premandibular, and according to Balfour probably belong to face-arches in that situation. The superior and inferior maxillary divisions fork over the cleft of the mouth, while the ophthalmic branch is connected with the third nerve in the ciliary ganglion.

The facial and auditory nerves appear to have a common origin. The main destination of the facial, as seen at an early period, is the hyoid arch, but it also sends forward a branch which is very large in young embryoes, forks over the hyo-mandibular cleft, and joins the inferior maxillary of the fifth in the mandibular arch as the chorda tympani of mammals. Besides this, two other branches

Fig. 745.

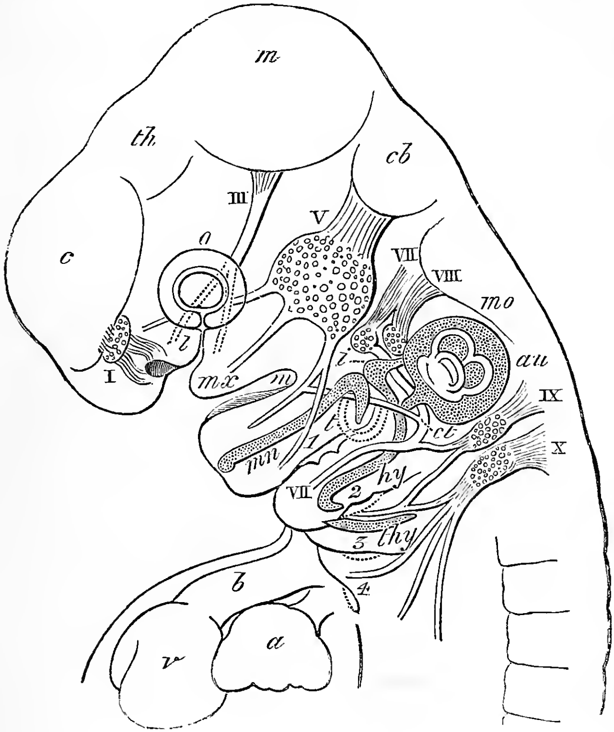


Fig. 745.—Outline diagram of the head of a mammalian embryo, corresponding to a human embryo of eight weeks, showing the relation of some of the principal cranial nerves to the visceral arches and the development of the ossicula auditus. (After A. Fraser, A.T.)

c, Cerebral hemispheres; *th*, thalamencephalon; *m*, midbrain; *cb*, cerebellum; *mo*, medulla oblongata; *o*, eye; *I*, olfactory ganglion and nerves passing to nasal cleft; *III*, third nerve; *V*, fifth nerve with Gasserian ganglion and its three branches; *VII*, facial nerve; *ct*, its chorda tympani branch; *VIII*, the auditory nerve; *IX*, glossopharyngeal nerve forking over the second postoral cleft; *X*, vagus; *l*, lachrymal cleft; *mx*, maxillary arch; *m*, mouth with indication of tongue; *mn*, mandibular cartilage with malleus forming in its proximal part; *i*, incus forming in the second cartilaginous arch; *t*, indication of the lower part of tympanic ring; *au*, the auditory capsule, semicircular canals, &c.; *hy*, hyoidean cartilage; *thy*, thyro-hyoidean cartilage; 1, 2, 3 and 4, indicate the places of the postoral clefts which are now closed; *b*, aortic bulb; *v*, ventricles of the heart; *a*, left auricle.

proceed forward from the facial, which are proportionally large in the embryo, viz., the superficial ophthalmic and the palatine (or superficial petrosal), which are respectively associated with the ophthalmic and superior maxillary divisions of the fifth nerve.

The auditory nerve, which proceeds at once to join the labyrinth of the ear, has a ganglion developed upon it at a very early period.

The glosso-pharyngeal nerve is connected with the third visceral or first true branchial arch, and in the lower vertebrates the pneumo-gastric or vagus is distributed to this and the branchial arches which follow in whatever number they may be. These nerves have in the chick a common origin from the dorsal neural crest of the after-brain, but, like the other nerves previously mentioned, they afterwards shift downwards so as to be placed on the sides.

According to Balfour some of the cranial nerves, such as the third, fifth and facial, besides the glossopharyngeal and vagus, may be held to bear definite relations to mesoblastic somites or muscle plates of the head, each being placed immediately behind the head-cavity of its respective somite. As stated by Parker, this relation is the following. Each of these nerves divides or forks above a visceral cleft, one division going to the posterior face of the arch in front of the cleft, the other to the anterior face of the arch behind it.

Fig. 746.

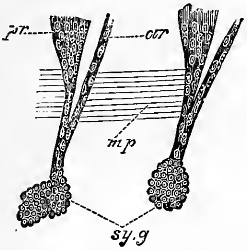


Fig. 746.—Longitudinal vertical section through part of the body-wall of an elasmobranch embryo showing two spinal nerves and the sympathetic ganglia belonging to them. (From Balfour.)

ar, anterior root; *pr*, posterior root; *sy.g*, sympathetic ganglion; *mp*, part of muscular plate.

The orbito-nasal and the palatine divisions of the trigeminus belong to an anterior arch, the former above, the latter below the optic nerve. The superior maxillary division follows the palato-pterygoid arch, the inferior maxillary nerve accompanies the mandibular arch.

The facial nerve divides above the hyo-mandibular cleft, its anterior part (chorda tympani) going to the posterior side of the mandibular arch, and its posterior part to the outer or anterior side of the hyoid arch.

The glosso-pharyngeal nerve, by a similar division, goes by its anterior branch to the posterior side of the hyoid arch, and by its other division to the front of the first branchial or thyro-hyoid arch.

In the higher animals the pneumo-gastric nerve shows no close relation to the clefts, but in branchiate vertebrates it forks over the remaining gill clefts and supplies branches to the gill arches.

Sympathetic Nerves.—It has been ascertained by Balfour that the sympathetic ganglia and nerves arise in connection with the gangliated roots of the cranial and spinal nerves, and they may therefore be regarded as springing from the same neuro-epiblastic source. This fact has been confirmed for birds and mammals by Schenk and Birdsell (No. 207).

The gangliated cord of the sympathetic has been described and figured by Kölliker in the human fœtus of eight or ten lines long. The peripheral sympathetic nerves are also formed at a very early period, and are perceptible in a fœtus of three months.

The Suprarenal Bodies.—The belief of a relation subsisting between the suprarenal bodies and the sympathetic ganglia of the nervous system seems to have originated with Bergmann in 1839, and to have received confirmation on embryological grounds from Remak in 1847, who called these bodies "nerve glands." It has, in fact, been long known that they have not any connection either by their origin or their permanent structural relations with the Wolffian bodies or with the kidneys. Leydig showed (1853) that in the adult plagiostomes, ganoids and reptiles the organs which represent the suprarenal bodies of the higher animals consist of

two separate sets of parts, of which one is intimately associated with the sympathetic ganglia and contains ganglionic cells, while the other is of a different nature. Kölliker's observations in the human embryo (No. 28, i. p. 618) gave further support to the view of the nervous nature and origin of these bodies; and more recently the researches of Balfour in elasmobranchs, Braun in reptiles and Brunn in birds, have led the first of these authors to state confidently the general view that while in elasmobranchs and some others of the lower vertebrates (No. 32, Vol. II. pp. 548–9) the suprarenal bodies consist of two distinct parts, viz., one median and single which he proposes to call "interrenal" of mesoblastic origin, and the other paired and derived from the sympathetic ganglia, in the amniota these two sets of parts are combined in the paired organs which constitute the compound suprarenal bodies. The development of these two sets of parts is, however, distinct; that derived from the mesoblast being converted into the cortical part, and the substance which proceeds from the ganglia being enclosed within the first in the course of their development.

The development of the suprarenal bodies of mammalia has very recently been made the subject of investigation by Mitsukuri (No. 212) in the rabbit and rat, the result of which fully confirms Balfour's views, and shows that in these animals the medullary part of the suprarenal bodies arises by development from the sympathetic ganglia of the abdomen lying below the aorta, that the cortical substance is of a totally different nature and of mesoblastic origin, and that the two sets of parts are gradually combined in the course of their formation. The medullary or nervous substance is at first situated outside the cortical or mesoblastic element, but gradually insinuates itself into the interior, retaining, however, some connection with the neighbouring ganglia. In the lower vertebrates, as already stated, this combination has not taken place, the two components of the suprarenal bodies remaining distinct and separate.

III. PRINCIPAL ORGANS OF SENSE:

I. THE EYE.

Primary Development.—The embryonic structures forming the eyeball and its contents may be considered as proceeding from three sources, viz., 1st, by evolution or expansion from the medullary wall of the thalamencephalon, giving rise to the retina in its nervous and pigmental structure and to the optic nerve; 2nd, by involution and development of a part of the cuticular epiblast, forming the foundation of the lens and the epithelium of the conjunctiva; and 3rd, by the intrusion of mesoblastic elements between and around the other parts, so as to furnish the materials out of which are formed the external coverings of the eyeball, cornea and sclerotic, the fibrous and vascular choroid, the ciliary apparatus and iris, the capsule of the lens and the capsulo-pupillary membrane, the vitreous humour, and all the fibrous and vascular parts of the organ.

The very early formation of the *primary optic vesicles* has been already mentioned, p. 823. The bulging wall of the anterior primary vesicle which is thus projected outwards on each side gives rise, by the subsequent folding and changes which occur in it, to the nervous part of the eye, viz., the retina and optic nerve, together with the pigmental layer which comes to lie external to the retina. This folding takes place simultaneously with the development of the crystalline lens, which is the product of an involution of the cuticle or epiblast occurring on the outside of each primary optic vesicle. During the involution and enlargement of the lens, the wall of the primary optic vesicle comes to be depressed and doubled in upon itself, so as to form a cup-like hollow towards the exterior, the secondary optic vesicle, into which the lens is received, but without filling entirely its cavity. The outer plate or involuted portion of this cup or secondary optic vesicle becomes by

its further development and histological differentiation the nervous part of the retina, while the remaining inner or proximal plate is converted into its pigmental layer, and the stalk becomes the optic nerve in connection with the brain.

Fig. 747.

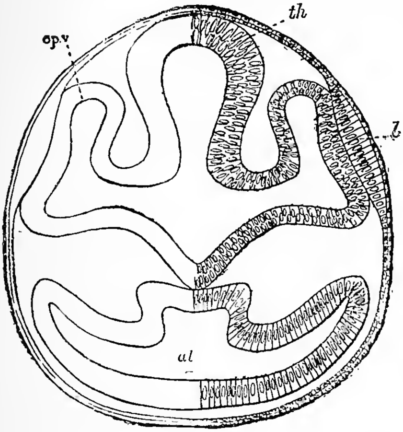


Fig. 748.

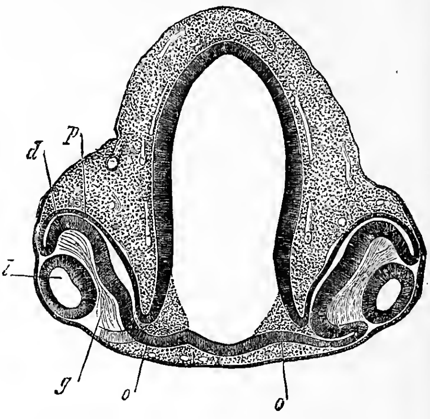


Fig. 747.—Section through the front part of the head of a Lepidosteus embryo. (From Balfour.)

al, alimentary tract ; *th*, thalamencephalon ; *l*, lens of the eye ; *op.v*, the optic vesicle.

Fig. 748.—Frontal section through the head of an embryo chick of 3 days and 6 hours. (From Kölliker.) $\frac{40}{1}$

o, stalk of the ocular vesicle in connection with the thalamencephalon ; *p*, proximal and *d*, distal wall of secondary ocular vesicle ; *l*, lens ; *g*, vitreous body.

The transition at the line of inflection from the thick nervous part to the thin pigmental part is quite sudden, and as soon as pigment cells begin to be developed a very marked distinction is perceptible between the latter and the nervous structure of the retina. These cells were formerly regarded as a part of the choroid membrane, but they are now looked upon as belonging rather to the retina,—a view which is fully warranted by the mode of development now described.

Fig. 749.

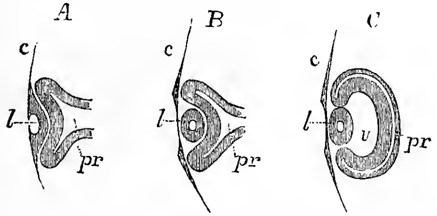


Fig. 749.—Section of the commencing eye of an embryo in three stages. (From Remak.)

A, commencement of the formation of the lens *l*, by depression of a part of C, the corneous layer ; *pr*, the primitive ocular vesicle now doubled back on itself by the depression of the commencing lens. B, the lens depression enclosed and the lens beginning to be formed in the inner side, the optic vesicle more folded back. C, a third stage, in which the secondary optic vesicle, *v*, begins to be formed.

The fold which produces the optic cup proceeds from above downwards, and surrounds the lens so as to appear to enclose it, but leaves

for a time an aperture or depression below. This is the *choroidal fold* or fissure, which may easily be distinguished in the embryo-head after pigment has been deposited, from the circumstance that the pigment is absent from the cleft, which thus appears for a time as a broad white line, particularly obvious in the embryo bird, running from the circumference in upon the lens.

Fig. 750.

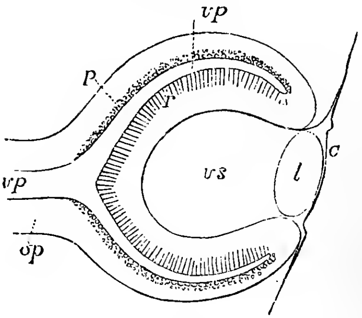


Fig. 750.—DIAGRAMMATIC SKETCH OF A VERTICAL LONGITUDINAL SECTION THROUGH THE EYEBALL OF A HUMAN FŒTUS OF FOUR WEEKS. (After Kölliker.) $\frac{100}{1}$.

The section is a little to the side so as to avoid passing through the ocular cleft. *c*, the cuticle, where it later covers the cornea; *l*, the lens; *op*, optic nerve formed by the pedicle of the primary optic vesicle; *vp*, primary medullary cavity of the optic vesicle; *p*, the pigment-layer of the outer-wall; *r*, the inner wall forming the retina; *vs*, secondary optic vesicle containing the rudiment of the vitreous humour.

The lens is developed in the part of the cuticle opposite to the most projecting part of the primary optic vesicle, or at the place where this vesicle comes in contact with the surface of the head. In this situation there is seen from a very early period a thickening of the epiblast, which seems to reside chiefly in its deeper layer of cells, and in birds and mammals it would appear that an actual involution of the cuticle takes

Fig. 751.

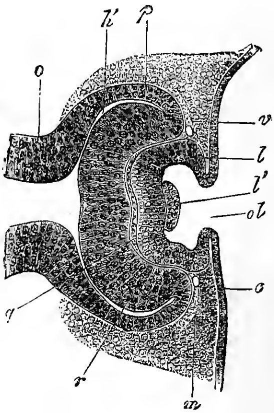


Fig. 751.—HORIZONTAL SECTION THROUGH THE EYE OF AN EMBRYO RABBIT OF TWELVE DAYS AND SIX HOURS. $\frac{70}{1}$. (From Kölliker.)

o, stalk of the ocular vesicle with wide cavity; *h′*, remains of the cavity of the primitive ocular vesicle; *p*, proximal lamella of the secondary vesicle (pigmentum nigrum); *r*, distal lamella (retina); *g*, vitreous body; *l*, lens vesicle, widely open at *ol*; *l′*, papillar elevation in the bottom of the lens vesicle which forms the lens; *m*, with *v*, an annular vessel at the anterior border of the secondary vesicle; *e*, epiblast.

place, so that first an open follicle and next an enclosed ball of cuticle is formed. Although, however, both the corneous and the deeper layer (sensory of Stricker) of the cuticle are enclosed, it is only the cells of the deeper layer which undergo development into the fibres of the lens. The external cuticle separating from the ball of the lens, passes freely over its surface, and a cavity filled with loose cells exists for a time within the lens. Then the cells of the hinder or inner wall are seen to rise from the bottom by their elongation, and thus a rapid growth of fibres from that side of the lens takes place, while the anterior or outer wall undergoes no similar change, but retains its simply cellular structure. Figures 751 and 752 show sufficiently clearly the manner in which the fibres thus

developed from cells rise from the bottom of the lens ball and come to constitute its solid part.

The optic cup receives the enlarging lens in its anterior and lower opening, and the reflected margins of the cup closely embrace the margin of the lens; but there soon comes to be a considerable space intervening between the lens and the hollow of the optic cup (or secondary vesicle), which is later occupied by the vitreous humour. Into this space

Fig. 752.

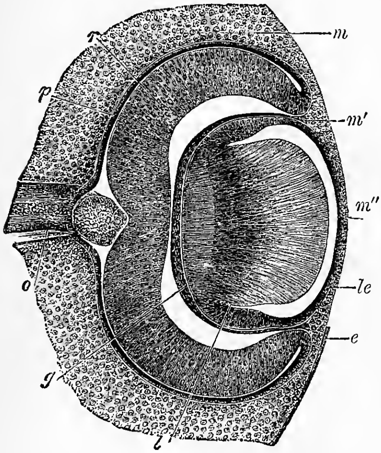


Fig. 752.—Eye of an embryo rabbit of 14 days; horizontal section. $\frac{65}{1}$. (From Kölliker.)

o, optic nerve; *p*, pigmentum nigrum; *r*, retina; *g*, vitreous body, which by its contraction has left a space behind it; *l*, posterior thick wall of the lens-vesicle, or rudiment of the lens; *le*, anterior thin wall or lens epithelium, and between them the hollow of the lens vesicle; *m*, mesoderm surrounding the secondary ocular vesicle, no sclerotic or choroid yet formed; *m′*, connection of this with the vitreous body; *m″*, thin layer of mesoderm in front of the lens or rudiment of the cornea and pupillary membrane; *e*, portion of the epithelium of the front of the eye.

connective tissue and blood-vessels developed from mesoblastic elements are projected from below, so as to furnish the materials for the formation of the vitreous humour and the blood-vessels which pass through it to the lens, and also to surround the lens with vascular and fibrous elements, out of which are produced the *capsulo-pupillary membrane*, and probably also the capsule of the lens. It results from the observations of Lieberkühn (No. 216) that in mammals the fold which produces the ocular cup or secondary vesicle runs back into the stalk so as to fold in the optic nerve for a considerable space, and by the simultaneous enclosure

Fig. 753.

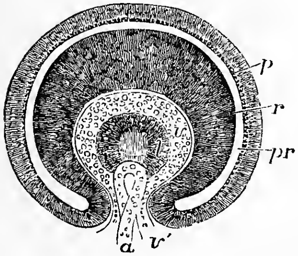


Fig. 753.—Transverse vertical section of the eyeball of a human embryo of four weeks. (From Kölliker). $\frac{100}{1}$.

The anterior half of the section is represented. *pr*, the remains of the cavity of the primary optic vesicle; *p*, the inflected part of the outer layer, forming the retinal pigment; *r*, the thickened inner part giving rise to the columnar and other structures of the retina; *v*, the commencing vitreous humour within the secondary optic vesicle; *v′*, the ocular cleft through which the loop of the central blood-vessel, *a*, projects from below; *l*, the lens with a central cavity.

of mesoblastic tissue thus to lead to the introduction of the central blood-vessels of the retina within the nerve. But in birds, according to the same observer, no such infolding of the stalk occurs, so that in them the vessels are excluded from the nerve. The malformation termed *coloboma*

iridis is to be attributed to a persistence of the choroidal cleft, and the pecten of birds, close to the optic nerve, with the vascular fold farther forwards, and the falciform fold of the eyes of fishes are to be regarded as fibro-vascular structures formed by original projection through the same interval.

The **further development** of the parts of the eye may be briefly stated as follows :—

The expansion of the ocular cup continuing to proceed, the chamber for the vitreous humour enlarges, and that structure gradually comes to occupy the space between the retina and the lens.

Fig. 754.

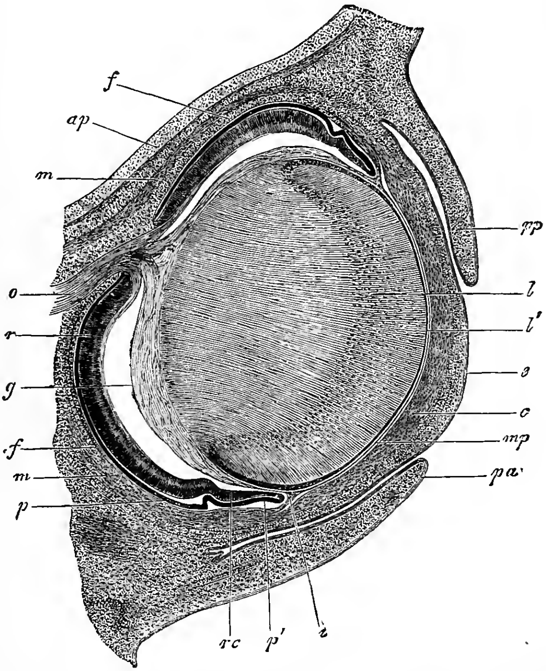


Fig. 754.—Horizontal section through the eye of an embryo rabbit of 18 days. $\frac{30}{1}$. (From Kölliker.)

o, optic nerve ; *ap*, ala parva ; *p*, pigmentum nigrum ; *r*, retina; *rc*, ciliary part of the retina ; *p'*, forepart of the secondary ocular vesicle or rudiment of the iris pigment ; *g*, vitreous body raised from the retina by shrinking, except where the vessels from the centralis retinæ enter it ; *i*, iris ; *mp*, membrana pupillaris ; *c*, cornea with epithelium *e ;* *pp*, *pa*, palpebræ ; *l*, lens ; *l'*, lens epithelium ; *f*, sclerotic ; *m*, recti muscles.

The marked distinction between the nervous and the pigmental portions of the primitive ocular vesicle goes on increasing by the continued deposit of pigment in the latter, and its proportional thinning, and by the great addition to the thickness and the textural differentiation of the substance of the former. Thus the cells in the retinal or nervous portion, by their rapid multiplication, soon become several layers thick; certain of these cells assume the spindle shape, and exhibit elonga-

tion into fibres, while others retain the nuclear form, and thus there is foreshadowed the division into the fibrous, ganglionic, and nuclear layers of the retina. On the exterior a limiting membrane makes its appearance, and in connection with it the rudiments of the cells composing the layer of rods and cones. The space between the retinal and pigmental layers rapidly contracts, and finally the rods and cones are closely united with the layer of pigment cells.

The optic nerve, as already described, is at first connected by its origin with the vesicle of the third ventricle or thalamencephalon, and for a time it retains its earlier hollow form. But as the cerebral hemispheres are developed forwards, the eye and the optic nerve are thrown backwards and downwards, and a new connection is established between the optic nerve (or tract) and the vesicle of the mid-brain (mesencephalon): the rudiment of the optic commissure is at the same time formed by the median approximation of the stalks and the growth of one over the other. Each stalk then becomes more and more solid by the development of nerve fibres and the formation of the sheath substance of the nerve from the enclosed connective tissue.

Retina and Optic Nerve.—The full development of the minute nervous structures of the eye is a subject of great difficulty, and observers are not quite agreed as to its phenomena. The rods and cones are undoubtedly formed in connection with the cells of the outer granular layer, but their outer and inner limbs are probably formed from different cells, the membrana limitans externa being at an early period placed between. According to Kölliker the layer of ganglion cells and the inner molecular layer are the first to be differentiated, and are very soon followed by the nerve fibres which spread over the interior of the retina. A somewhat different account of the process is given by Löwe (No. 222*), to whose work we must refer the reader.

At the ora serrata the denser nervous structure of the retina ceases, and in front of this, as far as the inflection of the distal into the proximal or pigmental layer, the retina is continued as the thinner ciliary portion, bounded externally by the pigment of the ciliary processes.

It has generally been held, and it is still the opinion of some, that the pedicle of the optic vesicle is converted into the optic nerve by the differentiation of its substance into nerve fibres. But a different view has been taken by His and by Kölliker (No. 28, i. p. 690) according to which the original substance of the pedicle is supposed to furnish only the supporting structures, and the nerve fibres are formed by secondary emanation from the chiasma or nervous centre.

According to Kölliker the yellow spot is not yet visible at birth.

Lens.—The development of fibres from the hinder wall of the primitive lens-follicle continuing to take place, the cavity of the follicle is first greatly narrowed and then completely filled up by the lengthening fibres, and the lens takes more and more of its full spherical shape. The new fibres continue to be formed towards the margin of the lens; each fibre retaining its nucleus, so as to produce the *nuclear zone* which runs through the whole lens. This zone is at first situated far back in the lens while the fibres are still short, but as they elongate its place is advanced, so that it comes to be situated considerably in front of the equatorial plane of the lens. It is most distinct towards the margin where the fibres are newly formed. The anterior wall of the lens-follicle remains as a simple cellular layer. The greater number of the fibres now follow the general curve of the surface of the lens, presenting therefore their concavity towards its centre, but the curvature gradually diminishes in those nearest the middle, where they are straight, or nearly so. Only the external short and recently formed fibres present a concavity towards the exterior. The intersecting stars of the anterior and posterior poles of the lens now make their appearance by the collection of cells in the peculiarly shaped triradiate or multiradiate space in these

two situations, and the ends of the fibres are now traceable to the edges of these spaces, so that the fibres gradually take the arrangement round the poles of the lens which belongs to the adult.

The origin of the capsule of the lens appears to be still somewhat doubtful. Lieberkühn, Arnold and Löwe profess to trace it to a thin pellicle of mesoblast which at an early period passes in between the lens and the secondary ocular vesicle; but Kölliker and Kessler are of opinion that it is a cuticular deposit on the surface of the lens cells. Balfour is inclined to adopt the latter view, on the ground that the capsule seems to make its appearance before the introduction of the mesoblast has occurred.

The *fibro-vascular structures* of the eye, which are all derived from mesoblastic elements, either surrounding the secondary ocular vesicle or passing into it by the choroidal fissure, may be considered as consisting of three sets of parts, viz., 1st, that which is external to the ocular cup and which becomes the sclerotic, the cellular substance of the cornea and also the choroid membrane; 2nd, that which occupies the interior of the optic cup, and which becomes the vitreous humour, and the capsulo-pupillary membrane with the arteria centralis retinæ; and 3rd, that which is developed in the angle of meeting of the two parts previously mentioned, *i.e.*, between the margin of the lens and the reflection of the two layers of the optic cup, and in which the ciliary processes, ciliary muscle and iris are mainly formed. The pigmental elements which any of these parts possess are derived from that of the retina or proximal wall of the optic cup.

Cornea.—The formation of the cornea is mainly due to a differentiation of the tissue in the layer of mesoblast which is interposed between the primitive lens-follicle and the corneous epiblast. The layer forming the cornea is at first very thin, and quite homogeneous, and it has been doubted if this is mesoblastic; soon, however, the corneal cells, proceeding from mesoblast which advances from the margin, penetrate the homogeneous layer, and gradually progress towards the centre, greatly thickening it, and dividing it into layers. The original homogeneous substance which is left free of cells at its margins constitutes the outer and inner elastic layers. Within these is the cellular layer of the membrane of Descemet, which comes from a different source. There is at first no aqueous chamber in the eye, and even after the solution of continuity which gives rise to this space has occurred, the cavity is not dilated with fluid, till near the time of birth. Even then it is very shallow and the lens is placed close to the cornea, in the greater part of its surface. The cavity of the aqueous humour arises by the separation of the cornea from a layer of the mesoblastic tissue lying within it. The latter gives rise to the anterior part of the vascular capsulo-pupillary membrane.

Sclerotic Coat.—The outer covering of the eyeball is formed from mesoblastic cells surrounding the ocular cup, and is probably continuous with the structure which furnishes the corneal cells, but it is only later that the cornea and sclerotic come to be completely amalgamated.

Choroid membrane.—The mesoblastic substance which surrounds the ocular vesicle externally is the source of important parts. Among these may be mentioned first the choroid membrane, the cellular (membrana fusca), fibrous, and vascular layers of which are developed out of the deeper division of the mesoblastic substance, and to the same source may be traced the ciliary processes, ciliary muscle and iris; while the zonula ciliaris may be regarded as a part of the deeper mesoblastic tissue connected with the formation of the hyaloid membrane and membrana capsulo-pupillaris.

The **capsulo-pupillary membrane**, already referred to, may be looked upon as at first a complete fibro-vascular investment of the lens, which owes its origin to the deepest part of the enclosed mesoblast. The vessels of this membrane are supplied by a branch of the central artery of the retina, which passes forwards in the axis of the globe, and breaks up at the back of the lens into a brush of rapidly subdividing twigs. The forepart of this tunic, adherent to the pupillary margin of the iris, forms the *pupillary membrane* by which the aperture of the pupil is closed in the middle periods of fœtal life. In the human eye, the whole tunic, together with the artery which supplies its vessels, becomes atrophied and is lost sight of before birth, but in some animals it remains apparent for a few days

after birth. According to Kölliker, the anterior chamber expands only a short time before birth by the intervention of the aqueous humour between the iris and cornea.

Fig. 755.

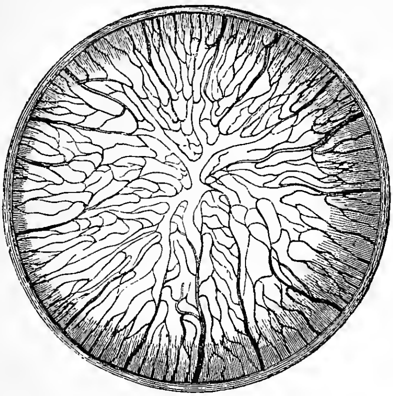


Fig. 755.—Blood-vessels of the capsulo-pupillary membrane of a new-born kitten, magnified. (From Kölliker.)

The drawing is taken from a preparation injected by Tiersch, and shows in the central part the convergence of the network of vessels towards the centre of the pupillary membrane.

The iris is developed from a proliferation of mesoblastic tissue which takes place in the angle between the anterior reflection of the walls of the ocular cup and the margin of the lens and cornea, and it is intimately connected with the capsulo-pupillary membrane, with which, indeed, it appears to be continuous anteriorly. It is thus in relation with all the fibro-vascular structures of the eye. It derives its pigmental layer from a reduplication of the anterior part of the pigmental layer of the ocular cup. It does not acquire free surfaces till after the formation of the aqueous chamber.

The ciliary muscle is developed in the mesoblastic tissue between the base of the iris and the ciliary processes of the choroid membrane.

Vitreous Humour and Hyaloid Membrane.—These parts are usually regarded as being derived from the intruded mesoblast; but while this may be true of the vitreous humour and the blood vessels which pass through it to the back of the lens, there are grounds for believing the hyaloid membrane to be derived by cuticular exfoliation from the ocular cup. The zonule of Zinn probably belongs to the same set of parts.

The **eyelids** make their appearance gradually as folds of integument, subsequently to the formation of the globe in the third month of fœtal life. When they have met together in front of the eye, their edges become closely glued together by an epithelial exudation which is removed a short time before birth.

The **lachrymal canal** may be regarded as a persistently open part of the fissure between the lateral nasal process and the maxillary lobe of the embryo.

The first discovery of the mode of development of the eye as it is now generally understood was made by Huschke in 1832, and was published in Meckel's Archiv. for that year. In addition to the systematic works on Development, the reader is referred to the special treatises mentioned in the Bibliography.

II. THE EAR.

Primary Development.—The most important part of the organ of hearing originates by the involution of the epiblast from the external surface of the head in the region of the medulla oblongata. This is at first only a depression of a thickened part of the epiblast; but the depression soon deepening, and, its aperture towards the surface rapidly narrowing, it assumes a flask-like form, and constitutes on each side the primary auditory or otic vesicle.

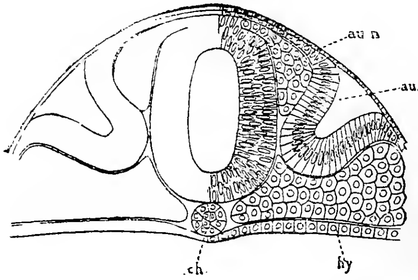
This involution of the auditory vesicle takes place somewhat later than the evolution of the medullary vesicle of the eye, and differs from it in taking place secondarily from the epiblastic surface of the head,

and not in immediate connection with the brain. The auditory vesicle is situated opposite the dorsal end of the hyoidean arch. The original

Fig. 756.—SECTION THROUGH THE HEAD OF A LEPIDOSTEUS EMBRYO OF AN EARLY PERIOD. (From Balfour.)

au.v, auditory vesicle ; *au.n*, auditory nerve ; *ch*, the notochord, immediately below the medulla oblongata ; *hy*, hypoblast. The nervous layer of the epiblast is seen to be distinct from the cuticular layer which is not involuted.

Fig. 756.



aperture, which is directed backwards, is soon closed externally, but in the interior a vestige of it remains for a considerable time as the *recessus labyrinthi*, which corresponds to the aqueduct of the vestibule of later life.

The primary otic vesicle, sinking down towards the basis of the cranium, becomes imbedded in the formative mesoblastic tissue lying between the basi-occipital and alisphenoid matrices, and along with them undergoes chondrification and ossification at an early period, as has been already described under the development of the head.

Fig. 757.

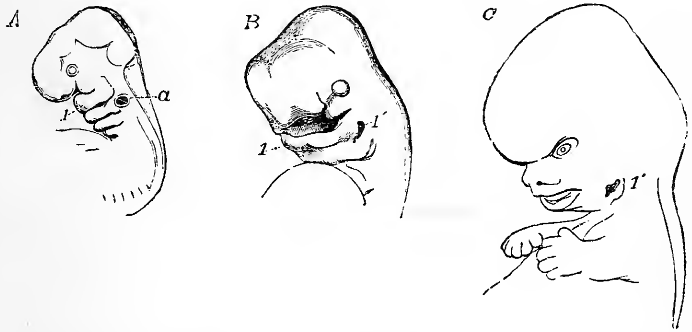


Fig. 757.—OUTLINES SHOWING THE EARLY CHANGES IN THE FORM OF THE HEAD OF THE HUMAN EMBRYO.

A, profile view of the head and fore part of the body of an embryo of about four weeks (from nature, $\frac{10}{1}$) : the five primary divisions of the brain are shown, together with the primary olfactory and optic depressions, and *a*, the auditory vesicle ; 1, marks the mandibular plate, and behind this are seen the three following plates with the corresponding pharyngeal clefts. *B*, from an embryo of about six weeks (from Ecker, $\frac{5}{1}$) : the cerebral hemispheres have become enlarged and begin to spread laterally ; 1, the lower jaw ; 1′, the first pharyngeal cleft, now widening at the dorsal end, where it forms the meatus externus ; the second cleft is still visible, but the third and fourth clefts are closed and the corresponding arches have nearly disappeared. *C*, from a human fœtus of nine weeks (from nature, $\frac{3}{1}$) ; the features of the face are now roughly formed ; the outer part of the first pharyngeal cleft is now undergoing conversion into the meatus, and the auricle is beginning to rise at its external border.

The development of the organ of hearing, as a whole, consists of two very different sets of processes, viz., 1st, those connected with the

formation of the nervous structure or labyrinth of the internal ear, and 2nd, those belonging to the development of the tympano-Eustachian passages and the accessory parts of the middle and outer ear. The first of these sets of changes occurs more immediately in the primary epiblastic vesicle in combination with the nervous elements derived from the medullary centre, and with the participation of the mesoblastic wall of the auditory capsule. In the second are involved the remarkable transformations of the first visceral arch and the hyomandibular cleft. In describing these changes reference will be made chiefly to mammals.

Labyrinth.—After the closure of the primary otic vesicle the extension of its cavity in different directions soon indicates the formation of the different parts of the future labyrinth. As the otic vesicle sinks more deeply into the base of the cranial wall, from being at first spherical it takes more of a pyriform shape, the pointed prolongation of the recessus labyrinthi stretching backwards or dorsally towards the place of the original involution from the surface.

Fig. 758.

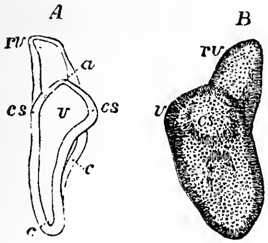


Fig. 758.—Labyrinth of the human fœtus of four weeks, magnified. (From Kölliker.)

A, from behind; B, from before; *v*, the vestibule; *rv*, recessus labyrinthi, giving rise later to the aqueduct of the vestibule; *cs*, commencement of the semicircular canals; *a*, upper dilatation, belonging perhaps to another semicircular canal; *c*, cochlea.

This narrower part soon becomes tubular, and stretches into the cranial wall, which it pierces, and in which, as the aqueduct of the vestibule, it becomes enclosed at a later period in the substance of the petrous bone. In elasmobranch fishes it remains open to the surface throughout life.

The auditory vesicle is also soon prolonged into an angular projection at its lower or ventral end, where it forms the commencement of the cochlear part of the labyrinth.

The two superior semicircular canals next appear as elongated elevations of the surface of the primary vesicle; the middle portion of each elevation becomes separated from the rest of the vesicle by the bending in of the walls under it, and thus the elevation is converted into a tube remaining open at both ends, which subsequently becomes elongated and acquires an ampullar dilatation; and while the cochlear extension continues to progress, and takes the form of a canal curving inwards, the external or horizontal semicircular canal begins to be formed much in the same manner as the two superior ones.

These changes are followed by a marked constriction of the main part of the vesicle on its inner side near the cochlear canal, which, gradually increasing, at last completely cuts off the part which afterwards becomes the *saccule* from the remaining larger portion which forms the *utricle*. A constriction also takes place in the vesicular wall between the saccule and the cochlear canal, leaving, however, these two cavities in communication by the narrow *canalis reuniens*.

The same constriction which separated the saccule and utricle leads to the division of the end of the recessus labyrinthi into two tubes, one of which now opens into each of these cavities.

The anterior or ventral part of the membranous labyrinth which is to form the foundation of the cochlea in mammals becomes soon elongated into a tube which is gradually bent inwards and coiled upon itself from

Fig. 759.

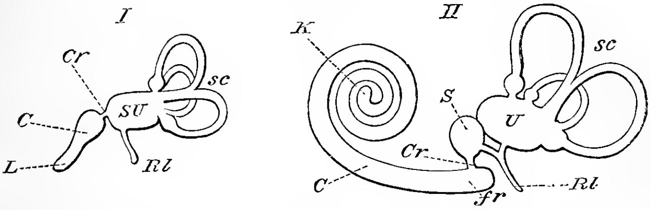


Fig. 759.—Diagrams of the membranous labyrinth (after Gegenbaur.)

I, in a bird ; II, in mammals ; *sc*, semicircular canals ; U, utricle ; S, saccule ; (SU. combined in I) ; R*l*, recessus labyrinthi ; *Cr*, canalis reuniens ; C, cochlea ; *fr*, its commencement at fenestra rotunda ; K, cupola ; L (in I) lagena.

left to right, at last to the extent of two and a half turns, and on the hollow side of this spiral there is now formed a double ridge of thickened epithelium which at a later stage is converted into the organ of Corti and the structures connected with the lamina spiralis.

Fig. 760.

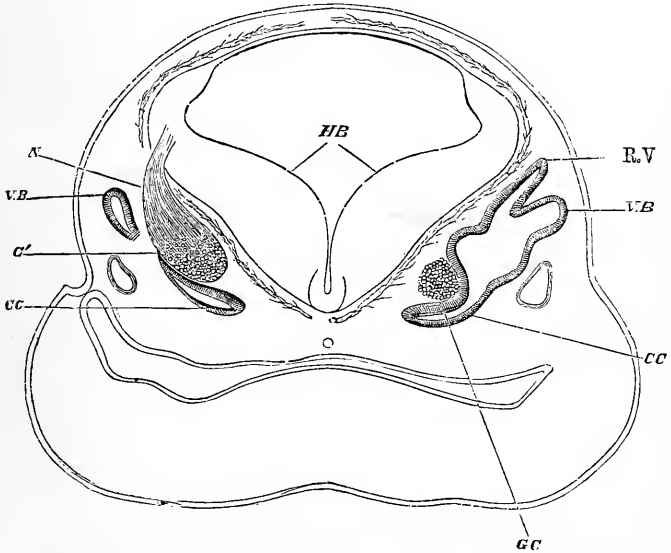


Fig. 760.—Transverse and slightly oblique section of the head of a fœtal sheep, in the region of the hind brain (from Foster and Balfour after Boettcher.)

HB, inner surface of the thickened walls of the hind brain ; RV, recessus vestibuli ; VB, commencing vertical semicircular canal ; CC, canalis cochleæ, with the cavity of the primitive otic vesicle. On the left side parts only of these structures are seen ; GC, cochlear ganglion of the right side ; on the left side, G′, the ganglion, and N, the auditory nerve connected with the hind brain.

Meanwhile, however, it may be mentioned that the deposit of cartilage has advanced rapidly in the auditory capsule surrounding the vesicle, and this is soon followed by ossification of the capsule, as elsewhere stated. But between the cartilaginous wall and the various parts of the membranous labyrinth mesoblastic tissue has been interposed, which gives rise to the periosteum and to the lymph spaces which surround the membranous labyrinth and contain the fluid termed perilymph; while the various inflections of the labyrinthic cavity which are of epiblastic origin are filled with the endolymph.

Fig. 761.

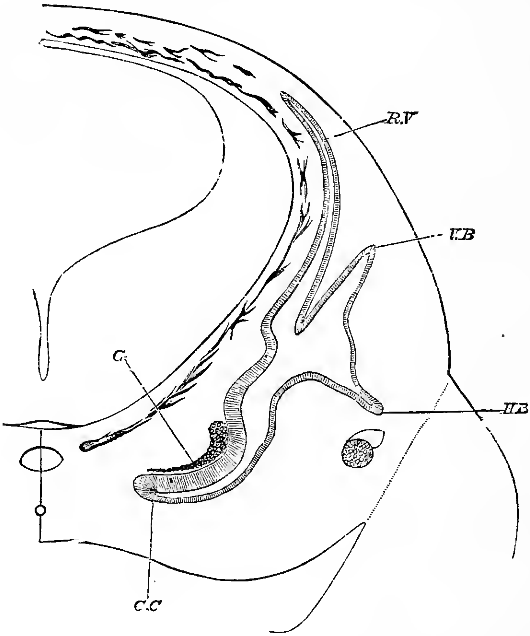


Fig. 761.—Transverse section of the head of a fœtal sheep of four-fifths of an inch in length. (From Foster and Balfour after Boettcher.)

RV, recessus vestibuli; VB, vertical semicircular canal; CC, cochlear canal; G, cochlear ganglion; HB, horizontal canal.

In the cochlea these spaces also exist, but in the special form of two tubular prolongations, one of which is situated on each side (above and below) of the cochlear canal, representing the first form of the scala vestibuli and scala tympani. Of these lymph passages the upper communicates with the vestibule, but the lower or scala tympani, which is somewhat later in being formed, is closed at the fenestra rotunda. The scalæ gradually progress along the coils of the cochlear canal till they reach its summit or *cupola*, which at first adheres to the wall of the capsule. From this, however, it is afterwards separated, when the two scalæ, having arrived at the summit, communicate with each other and intervene between the cupola and capsular wall.

The *lagena* of the uncoiled cochlea of birds corresponds to the cupola of the cochlear canal in mammals.

The lamina spiralis, with the organ of Corti and the upper and lower separating membranes (membrane of Reissner and membrana basilaris), are afterwards gradually developed outwards from the central pillar of the coiled cochlea; but we cannot attempt to give any detailed account of the formation of these minute and intricate structures.

Fig. 762.

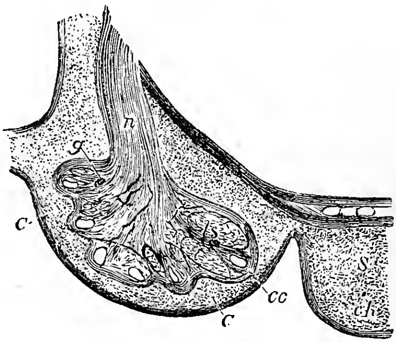


Fig. 762. — Transverse section of the cochlea in a fœtal calf, magnified. (From Kölliker.)

C, the wall of the cochlea, still cartilaginous; *cc*, canalis cochleæ; *ls*, placed in the tissue occupying the place of the scala vestibuli, indicates the lamina spiralis; *n*, the central cochlear nerve; *g*, the place of the spiral ganglion; S, the body of the sphenoid; *ch*, remains of chorda dorsalis.

It may, however, be mentioned that the auditory nerve when first formed is of large size and pierces the auditory capsule in two main divisions, vestibular and cochlear. The latter is remarkable as having upon it at an early period a large ganglion which exists before the cochlea becomes coiled, but which, being developed along with the lamina spiralis, takes the same coiled form (see fig. 761, and p. 466 of this volume).

The modiolus and spiral lamina, according to Kölliker, are ossified without the intervention of cartilage.

Accessory Parts of the Organ of Hearing.—The remarkable combination of the internal ear, or labyrinth, with certain other parts, to form the middle and external divisions of the acoustic apparatus, has already been adverted to in the account of the development of the face. Here, without going over the whole subject, we shall have only to refer shortly to some points of morphological interest connected with it.

The **tympano-Eustachian** passage is generally held, according to the view first propounded by Huschke, and confirmed by Reichert and others, to be developed in connection with the inner part of the hyo-mandibular or first postoral visceral cleft, while the meatus externus and pinna, or auricle, are formed on the outside; the membrana tympani, with its tympanic ring being interposed between, and the chain of ossicula with their accessory parts being formed in close relation with them. There can be no doubt that this view is substantially correct. But more recent researches, besides giving greater precision to the facts, have also modified in some degree the history of the process. From these researches it appears that the tympanic ring and the membrana tympani are developed close to the external surface, and that the meatus is therefore formed more immediately in connection with the outer skin, and by outward growth of the parts surrounding it, rather than by any actual depression.

Further, it is ascertained by the observations of A. Fraser that the hyo-mandibular cleft is from an early period almost completely closed in its dorsal portion by the intervention of the membrana tympani. This membrane consists of a layer of epiblast externally, of pharyngeal hypoblast internally, and, between these, of its fibrous and vascular parts, which are of mesoblastic origin.

According to the same author (No. 230), the malleus, as now agreed

by all, is developed from the proximal part of the mandibular cartilage, and by observations on a variety of mammals he has shown that the incus is formed, according to the view advocated by Huxley and Parker, and contrary to that of Reichert, Salensky and others, in the proximal part of the hyoidean cartilage, which, from the first, is in close proximity to the mandibular cartilage. Fraser has further shown, in corroboration and extension of Salensky's observations (No. 229), that the stapes does not arise as a part of the hyoidean cartilage, or as a bud from the periotic wall, but as a circular deposit of cartilaginous cells round the stapedial artery, near to the fenestra ovalis, with which its base is afterwards connected.

With respect to the precise mode in which the tympanic cavity and Eustachian canal are formed in relation with the hyo-mandibular cleft, some difference of opinion has arisen among recent observers. Some, as Moldenhauer and Hunt (Nos. 222 and 228), have brought forward the view that these parts of the auditory passages are one or both of them new outgrowths from the pharynx, and others (Urbantschitsch), that they proceed from the mouth. But these authors do not give sufficient grounds for departing from the generally accepted opinion on this subject.

The **pinna** is gradually developed in connection with the integument on the posterior margin of the first visceral cleft. It is deserving of notice that congenital malformation of the external ear, with occlusion of the meatus and greater or less imperfection of the tympanic apparatus, are observed in connection with abnormal development of the deeper parts of the first and second visceral arches and the intermediate cleft (Allen Thomson, No. 231).

III. THE NOSE.

The organ of smelling, as was first pointed out by v. Baer, owes its origin, like the primary auditory vesicle and the crystalline lens of the eye, to a depression of the epiblast, and it differs from these involutions in remaining permanently open and in being greatly extended as a complicated cavity communicating with the exterior.

It has already been shown how closely the development of the nose is connected with, first, the extension of the axial part (trabeculæ) of the basi-facial axis; second, the formation of the mouth, so that a part of the common cavity comes to be separated by the palate plates into the true buccal and lower nasal cavities; and, third, more superficially and in front, with the external nasal wall.

The olfactory organ arises in all vertebrates at a very early period of embryonic life in the form of a depression of thickened epiblast from the forepart of the head.

The whole of the nasal fossæ, however complicated they may become in the labyrinthic form which they afterwards assume in many animals, are due to the involution of the epiblast of the original olfactory pits; and the structure of the parts forming these inflections, as well as those associated with them, which are derived from mesoblastic sources, may be considered as essentially the same in different animals. In man these structures do not attain any great degree of complexity in the olfactory part, but in the human nose, as in animals, there is a marked difference in the form of that part of the labyrinth on which the olfactory nerve is distributed, and in the minute structure of its epithelium, from those of the lower part which forms the respiratory passage of the nose.

There is at first no olfactory lobe of the brain, and the nerve is solid. Marshall has shown that the olfactory lobe is formed at a comparatively late period, as at the end of the seventh day in the chick, and that this lobe arises by extension of the wall of the forebrain at the place

where the nerves have previously sprouted out; that it contains a hollow prolonged from the general ventricular cavity, and carries the nerves on its most projecting part.

The development of the olfactory nerve has already been described.

III. DEVELOPMENT OF THE BLOOD-VASCULAR SYSTEM.

General Phenomena.—The heart and blood-vessels, with the blood-corpuscles and fluid, which from the first occupy their interior, take their origin entirely from the mesoblast, and the earlier rudiments of these

Fig. 763.

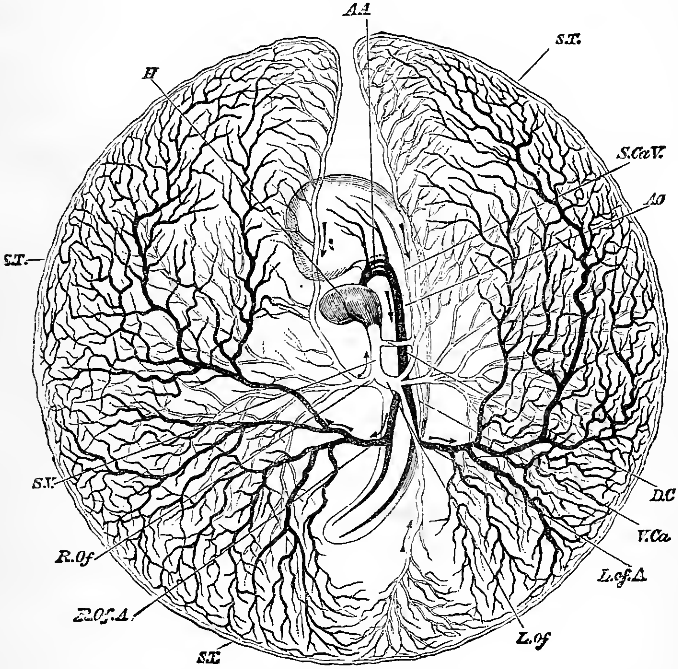


Fig. 763.—Vascular area of the yolk-sac of the chick on the third day of incubation, seen from below. Magnified about six diameters. (From Balfour.)

H, heart; *AA*, three of the aortic arches of one side; connected with the uppermost are the external and internal carotid arteries; *AO*, dorsal aorta; *L.of.A*, left vitelline artery; *R.Of.A*, right; *S.T.*, Sinus terminalis; *L.Of*, left vitelline vein; *R.Of*, right; *S.V.*, sinus venosus; *D.C*, Ductus Cuvieri; *S.Ca.V*, superior cardinal vein; *V.Ca*, inferior; the arteries are shaded black, the veins are in outline; the embryo seen from its lower or left side is only faintly indicated.

vascular elements are situated in the deepest part of the visceral plate of the mesoblast, which was thence distinguished by Pander as the vascular layer of the blastoderm. At a later period it is probable that blood-vessels may arise throughout the whole of the mesoblast, both in its visceral and parietal divisions.

The simultaneous origin of the blood-vessels and heart, partly within the body of the embryo and partly in the vascular area of the yolk, appears to be universal throughout the vertebrata, and is only modified in form in a few instances, as in some of the amphibia, by the undeveloped condition of the yolk sac. In the human ovum the same appears to be the first condition of the blood-vascular system, and as soon as before the fourteenth day from conception a simple tubular

Fig. 764. A

B

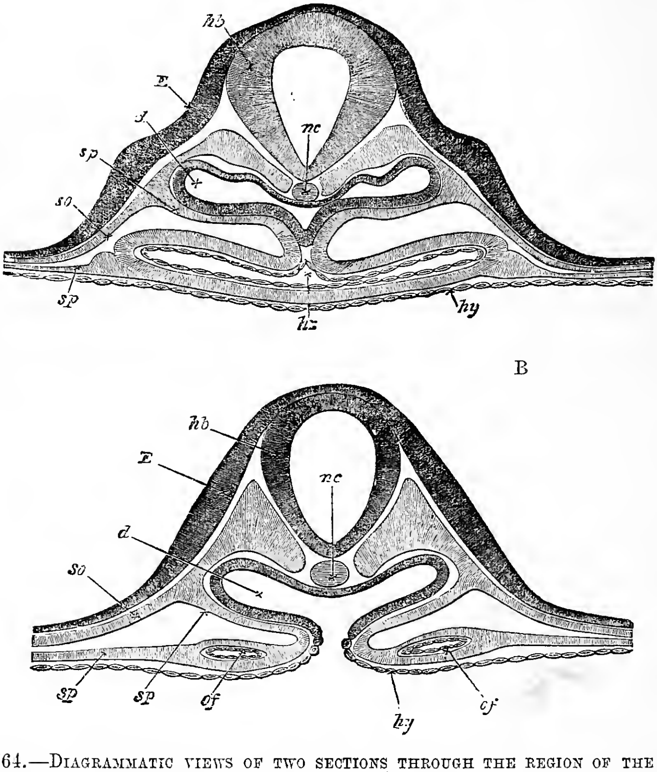


Fig. 764.—Diagrammatic views of two sections through the region of the hind-brain of an embryo-chick of about 36 hours, illustrating the formation of the heart. (From Balfour.)

In A, which is farthest forward, the parts of the heart have coalesced in the middle ; in B, which is farther back, they are still widely separate.
hb, hind-brain ; *nc*, notochord ; *E*, epiblast ; *so*, body-wall ; *sp*, visceral wall ; *d*, alimentary canal ; *hy*, hypoblast ; *hz*, heart ; *of*, vitelline veins.

heart with incoming and outgoing vessels are formed in the body of the embryo, while the surface of the yolk or umbilical vesicle is occupied by ramified vessels and their capillary network.

The phenomena of vascular and blood formation have been observed with great minuteness and care, as they occur in the egg of the common fowl in the first half of the second day of incubation, and a sufficient amount of observations have been made in mammals and other animals

to prove that the process is essentially the same in them all. The earlier steps of this process follow one another very rapidly, so that already by the 40th or 42nd hour in the fowl's egg the blood is propelled through the primary system of vessels by the rhythmic contractions of the tubular and as yet only cellular heart. At this period the parts of this very simple circulatory system consist of the blood fluid containing corpuscles in a rudimentary form; of blood-vessels, which are mainly spread over the vascular area and in less number within the body of the embryo; and of a median tubular heart, into which the blood is brought from behind by two veins which collect it from the vascular area, and from which it is expelled anteriorly by two outgoing vessels which may be called arteries, though they do not as yet show any of the histological characters of these vessels.

The minuter steps of this process have been so fully described in the histological part of this work (p. 34 and p. 197), that it is unnecessary to do more at this place than to recall the fact that the blood-fluid and corpuscles originate by a change in the formative cells of the visceral mesoblast, which is accompanied by a differentiation of their protoplasm and multiplication of nuclei within spaces developed by internal vacuolization of the mesoblastic cells. The cells which give rise to the primary blood-vessels becoming hollow and radiated, and their processes being united together, capillary networks are produced by their dilatation into tubes and their intercommunication. The demarcation of the limits between the epithelial cells forming the walls of the primary capillary vessels is a later process, as also the addition of the cellular materials for the production of the middle and outer coats, and other tissues which give a more complex structure to the larger vessels: but nearly all the vessels consist at first only of endovascular elements, and have much of the form and structure of capillaries.

I. THE HEART.

The origin of the heart itself is in some respects histologically similar to that of the vessels, in so far that it is by the vacuolated formation of one or of two main tubular spaces within groups of mesoblastic cells that the cavity of the organ originates (see fig. 744, p. 838). But the formation

Fig. 765.

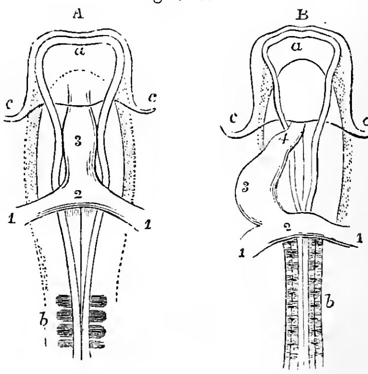


Fig. 765.—Outlines of the anterior half of the embryo chick viewed from below, showing the heart in its earlier stages of formation. (After Remak.) $\frac{20}{1}$

A, embryo of about 28 to 30 hours; B, of about 36 to 40 hours; *a*, anterior cerebral vesicle; *b*, proto-vertebral segments; *c*, cephalic fold; 1, 1, vitelline or omphalo-mesenteric veins entering the heart posteriorly; 2, their union in the auricle of the heart; 3, the middle part of the tube corresponding to the ventricle; 4 (in B) the arterial bulb.

of the walls of the primitive heart is due, not merely to the accumulation and differentiation of the mesoblastic cells in the region which it at first occupies, but is also effected by a folding of the mesoblastic layers round the cavity. In these folds two sets of

cells are distinguishable from a very early period, viz., 1, those of a more delicate character and looser disposition in which the space or spaces for the heart's cavity are more immediately formed, and which afterwards range themselves round that cavity in the form of an endocardiac lining, and, 2, those forming a thicker layer which undergoes inflection, and which give rise to the muscular part of

Fig. 766.

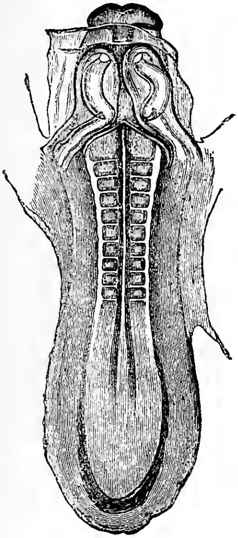


Fig. 767.

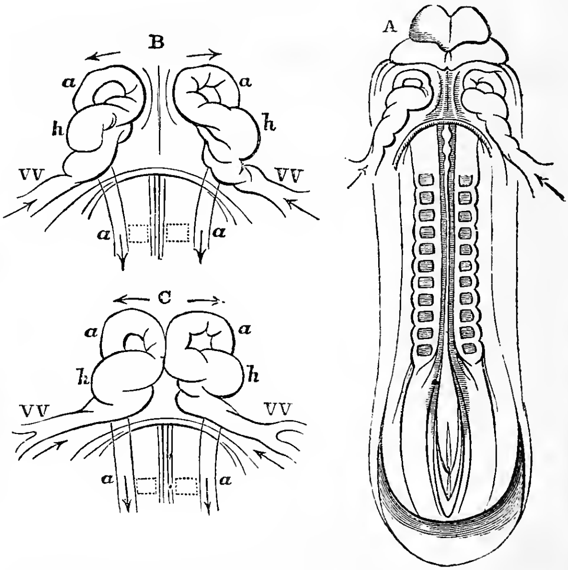


Fig. 766.—EMBRYO RABBIT OF EIGHT DAYS AND EIGHTEEN HOURS, VIEWED FROM THE VENTRAL ASPECT. $\frac{24}{1}$. (From Kölliker.)

In the anterior part of the ventral wall on each side there is seen the separate rudiment of the heart, in the simple vascular tube of which are to be distinguished the hinder auricular, the middle ventricular and the anterior bulbous parts. There are ten proto-vertebral segments.

Fig. 767.—VIEWS FROM BELOW OF THE EMBRYO-RABBIT OF NINE DAYS AND THREE HOURS, SHOWING THE COMMENCING HEART IN TWO STAGES. $\frac{22}{1}$. (A. T.)

These sketches, of which B and C are partly diagrammatic, were taken from two preparations given me by Professor Kölliker. A is the view from below of one of the embryoes in which the formation of the heart was least advanced, and of which an outline of the heart, &c., is repeated in B. In C, taken from the second preparation, the two halves of the heart are seen in the commencement of their coalescence. *h*, the part of the bent tube which becomes the ventricle ; *a*, primitive aortic arches and separate descending aortas ; VV, the vitelline veins entering the heart posteriorly. The arrows indicate the course of the blood.

the wall. The pericardial covering arises by an extension of the wall of the body cavity which folds itself round each side of the commencing part of the heart.

There is, however, a considerable difference among animals in the form presented by the rudiments of the primitive heart, connected apparently with a difference in the rate of progress of the cephalic fold of the blastoderm which incloses the anterior part of the alimentary canal, and the median coalescence of the parts which give rise to the

heart itself. Thus in certain animals, such as elasmobranchs, cyclostomata, ganoids, and amphibia, in which the closure of the cephalic fold is rapid, the deeper or endocardiac rudiments of the heart are collected into a mesial mass, and the cavity of the organ hollowed out in their interior is from the first single, and occupies a place on the ventral side of the pharynx immediately behind the branchial arches,

Fig. 768.

Fig. 768.—Transverse section through the head of an embryo rabbit of eight days and fourteen hours, with a part of the peripheral blastoderm. $\frac{48}{1}$. (From Kölliker.)

hh, rudiments of the heart; *sr*, pharyngeal groove.

where it receives the inflection of the mesoblastic cells, which form its muscular wall. But in others, such as mammals, in which the fact was first discovered by Hensen (No. 88), in osseous fishes, and to some extent also in birds, in which the enclosure of the pharyngeal cavity by the inflection of the cephalic fold is of later occurrence, the heart has at first the remarkable form of two tubes separated to some distance from each other, and the formation of the single and median cavity of the heart is due to the gradual approximation of these tubes and their coalescence

Fig. 769.

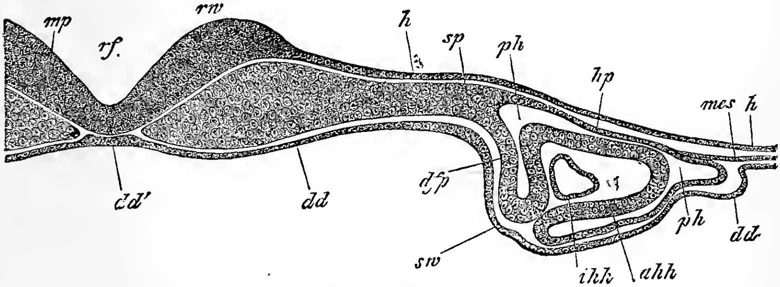


Fig. 769.—Part of the foregoing figure more highly magnified. $\frac{152}{1}$. (From Kölliker.)

rf, medullary groove; *rw*, dorsal ridge; *mp*, medullary plate and rudiment of the brain; *h*, epiblast; *hp*, parietal wall; *dfp*, visceral mesoblast, inflected into the outer wall of the heart *ahh*; *ihh*, inner or endovascular lining of the heart; *ph*, pericardial cavity; *mes*, mesoblast beyond the rudiments of the heart; *dd*, hypoblast; *dd'*, notochord; *sw*, lateral wall of the developing pharynx.

into one by the union and subsequent disappearance of the adjacent parts of their primitive walls. In the case of the heart being thus at first double, each tube receives posteriorly the large entering vein, and is prolonged anteriorly into the issuing vessel or artery; while in the median single heart, whether formed originally so, or by later fusion of two tubes, the posterior part receives the two entering veins, while the anterior part opens into the two primitive outgoing arteries.

The accompanying figures (768 & 769) from Kölliker will explain by a sectional view the manner in which in mammals the inflection of the two laminæ of the meso blast gives rise to the walls of the separate components

Fig. 770.

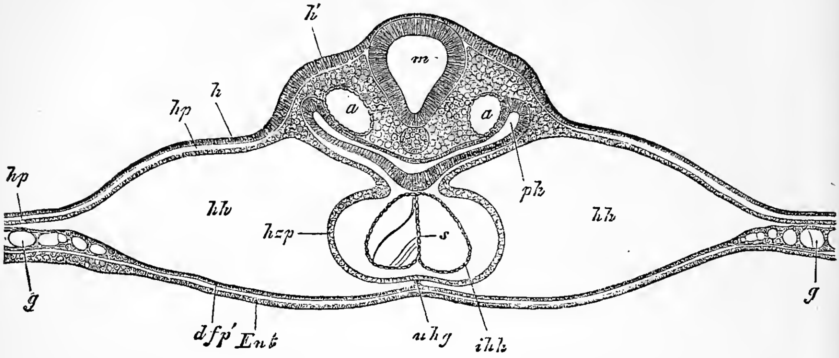


Fig. 770.—Transverse section through the region of the heart in an embryo-chick of 39 hours. $\frac{61}{1}$. (From Kölliker.)

m, medulla oblongata ; *a*, *a*, descending aortas ; *ph*, pharynx ; *h*, epiblast ; *h'*, thickening of the same where the auditory vesicle is to be formed ; *hp*, parietal mesoblast; *hzp*, outer wall of the heart ; *ihh*, inner wall, the cavity still divided by a septum *s* ; *hh*, pericardial cavity ; *uhg*, ventral mesocardium produced temporarily by the reflection of the visceral mesoblast *hzp* into *dfp'* ; *g*, *g*, vessels in the visceral mesoblast ; *Ent*, hypoblast.

of the heart and the primary right and left compartments of the pericardium. The endocardiac lining (*ihh*) is derived from the deeper part of the visceral mesoblast.

Fig. 771.

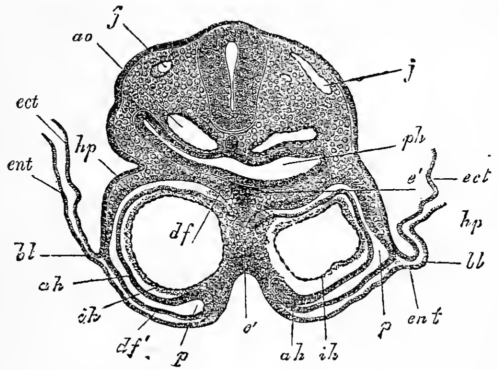


Fig. 771.—Transverse section through the region of the heart in a rabbit's embryo of nine days. $\frac{80}{1}$. (From Kölliker.)

jj, jugular veins ; *ao*, descending aortic roots ; *ph*, pharynx ; *hp*, body-wall reflected in *ect* ; *ih*, inner cellular lining of the still divided heart ; *ah*, outer wall of the heart ; *p*, pericardial cavity ; *df*, *df'*, visceral mesoblast ; *e'*, prolongation of the hypoblast of the foregut and the anterior wall of the pericardial cavity into the partition between the two halves of the heart ; *bl*, blastoderm ; *ent*, visceral wall.

It would appear that in both forms of the heart's origin the inflection of the mesoblast which gives rise to its wall is at first incomplete. In the case of the single and median formation this has the effect of leaving the endocardiac wall of the rudimentary organ in immediate contact with the hypoblast of the cephalic part of the alimentary cavity ; but very soon the further inflection of the

outer mesoblastic layer of cells completes the muscular and pericardial wall superiorly or on the dorsal side, leaving however there for a time a short septum at the place of meeting which constitutes a superior or dorsal mesocardium, while a similar septum exists for a time below as a ventral mesocardium.

The mode of formation of the heart in birds is in some degree intermediate between the two previously referred to, as the single organ arises by the coalescence of two tubes which are at first separate, but by the time these are formed the ventral wall of the pharynx is already advanced in its enclosure, so that it is almost impossible to detect the double form in the view of flat specimens of the bird's embryo. Hence. before the fact was ascertained by means of sections, the older observers all held the heart of the bird to originate as a single median organ.

The primitive veins or large vessels by which blood is carried into the posterior extremity of the rudimentary heart are the principal returning venous channels which collect the blood from the terminal sinus of the vascular area, while the two vessels which proceed from the anterior extremity form the first pair of aortic arches which bend over the side of the pharyngeal wall at the level of the mandibular arch and pass on dorsally in the body of the embryo below the vertebral somites as the two primitive aortæ, which afterwards coalesce to form the median aorta. To these further reference will be made later.

Among the further changes which the heart undergoes in the course of its progress from the simple form of a median symmetrical tube into

Fig. 772.

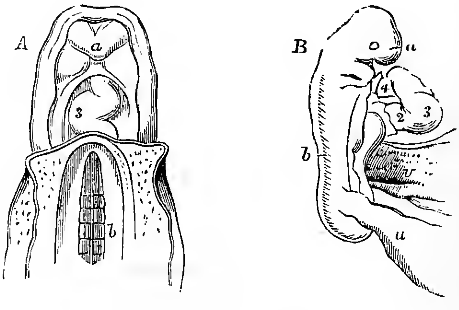


Fig. 772. — Human embryos at different early stages of development, showing the heart in its tubular condition.

A, upper half of the body of a human embryo of three weeks, viewed from the abdominal side (from Coste); *a*, frontal plate; *b*, protovertebræ, on which the primitive aortæ are lying; 3, the middle of the tube of the heart, below it the place of entrance of the great veins, above it the aortic bulb.

B, lateral view of a human embryo more advanced than that last referred to (from A. Thomson); *a*, the frontal part of the head; *b*, the vertebral column; *v*, the wide communication of the umbilical vesicle with the intestine; *u*, allantoic pedicle; 2, auricular part of the heart connected with the veins posteriorly; 3, ventricular part of the bent tube; 4, the aortic bulb; near the extremities of the tube the divided pericardium is seen.

its fuller state of development, one of the earliest may be attributed to the mere elongation of the tube, for the anterior and posterior extremities being fixed by the vascular connection to the body of the embryo, the elongating intervening part, which is not so attached, is necessarily thrown into a folded or curved shape, the middle part bulging ventrally, and taking usually a direction to the right side of the still prone and symmetrical embryo. This form of the heart has been observed in the human embryo of three weeks, corresponding in all respects to the heart of the bird or mammal at a parallel stage of advancement (see Fig. 772, A and B).

As the development of the tubular heart progresses, the bend increases, and the venous is doubled back upon the arterial end. The

tube also becomes divided by two slight constrictions into three portions, of which that originally posterior and receiving the veins is the widest, and constitutes the primitive auricle; the middle one, next in width, and most strongly bent upon itself, becomes the ventricular portion; and the third, situated anteriorly and retaining most the simple tubular form, is the arterial or aortic bulb.

Division into Single Auricle, Ventricle, and Arterial Bulb. —By a continued increase of the inflection of the heart-tube, a change in the relative position of the several parts is effected, so that the auricular cavity comes to be placed above or behind (dorsally) and to the left of the ventricular part, the veins being carried forwards along with it, while the arterial bulb is attached by its extremity in front to the neck of the embryo immediately below the visceral plates. There is as yet only a single passage through the heart, but the distinction of the auricular and ventricular cavities becomes more apparent, both by an increase in the diameter of each, and by the constriction which separates them, and by the much greater thickness acquired by the walls of the ventricular and bulbous parts as compared with the auricular portion.

Fig. 773.

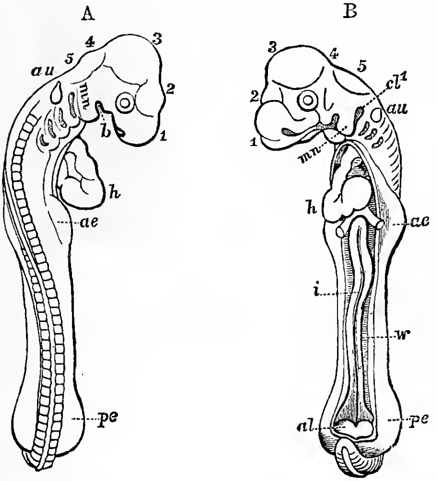


Fig. 773. — Outlines of the embryo of the chick at the end of the third day. $\frac{10}{1}$. (After His.)

A, dorsal and right side; B, ventral and left side; *h*, the heart. The other parts of the figure are explained elsewhere.

The three parts of the heart have now the appearance of being very closely twisted together. The ventricular part becomes considerably wider transversely, and the auricular part shows two projecting pouches, one on each side of the arterial bulb, which are the first indications of the future auricular appendages. At the same time the constriction between the auricular and ventricular parts increases considerably, and the constricted part elongating, produces what has been called the *canalis auricularis*.

Division of the Right and Left Cavities. Ventricles.—The next series of changes in the developing heart consists in the division of each original single cavity of the ventricle, auricle, and arterial bulb into two compartments, so as to form the right and left ventricles and auricles, and the stems of the pulmonary artery and aorta. The first of these changes occurs in the ventricular portion, and is to be seen in progress on the fourth day in the chick, and in the sixth and seventh week in the human embryo. The ventricular chamber of the heart increasing considerably in breadth, that part of it which ultimately becomes the apex of the heart is thrown towards the left side, and in most mammals, and especially in

the human embryo, a blunt cleft or depression appears between this and the right part of the ventricle, which causes an external division into two portions corresponding to the future right and left ventricles; and if the interior of the ventricular cavity be examined at this time, there is perceived a crescentic partition rising from the lower border of the right wall and projecting into the cavity, at first narrow and placed opposite the external notch, but gradually growing more and more towards the

Fig. 774.

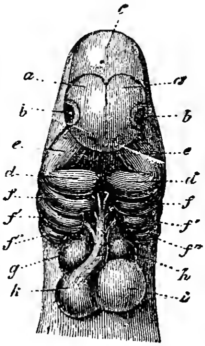


Fig. 774.—Head of the embryo of the dog with the heart seen from below. (From Kölliker, after Bischoff.) Magnified.

a, cerebral hemispheres; *b*, eyes; *c*, mid-brain; *d*, mandibular plates; *e*, superior maxillary processes; *f*, *f'*, *f''*, second, third, and fourth branchial or visceral plates; *g*, right, *h*, left auricle of the heart; *k*, right, *i*, left ventricle; *l*, aortic or arterial bulb, with three pairs of aortic or vascular arches proceeding from it.

auriculo-ventricular aperture. As development progresses the external division becomes more or less effaced, when the apex of the heart formed by the left ventricle becomes more pointed, and the whole heart takes somewhat of the conical form which belongs to its advanced condition; but in the adult heart the depression is still perceptible as the interventricular groove, which, as is well known, varies considerably in depth in different cases. In some animals, as the rabbit, the temporary external division of the ventricles is very apparent, while in others, as in

Fig. 775.

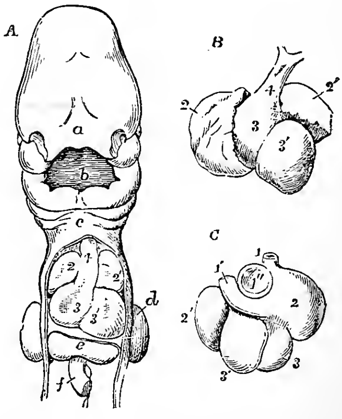


Fig. 775.—Shows the position and form of the heart in the human embryo from the fourth to the sixth week.

A, upper half of the body of a human embryo of nearly four weeks old (from Kölliker after Coste); B and C, anterior and posterior views of the heart of a human embryo of six weeks (from Kölliker after Ecker); *a*, frontal lappet; *b*, mouth; *c*, ventral ends of the second and third branchial arches; *d*, upper limb; *e*, liver; *f*, intestine cut short; 1, superior vena cava; 1', left superior cava or brachio-cephalic connected with the coronary vein; 1'', opening of the inferior vena cava; 2, 2', right and left auricles; 3, 3', right and left ventricles; 4, aortic bulb.

ruminants, there is very little of the external notching to be seen, and in them, as in birds, the heart very early assumes the conical form. The dugong presents a remarkable example of the persistence of the complete external separation of the ventricles, and in the seal a tendency has been observed to the occasional occurrence of the same variety (Ecker, A. Thomson).

The internal septum of the ventricles continuing to rise between the

right and left divisions of the cavity, reaches at last the base, where it is placed in relation with both the auriculo-ventricular orifice and the root of the arterial bulb; but at this place there remains for a time a communication over the still free border of the septum between the right and left ventricles, which is interesting, as this is the seat of the abnormal communication between the right and left ventricles in almost all cases of malformation of the heart presenting that condition.

Division of the Auricles.—Although the auricular cavity presents externally some appearance of being divided into two at a period antecedent to the partition of the ventricles, in consequence of the formation of the right and left auricular appendages before mentioned, the

Fig. 776.

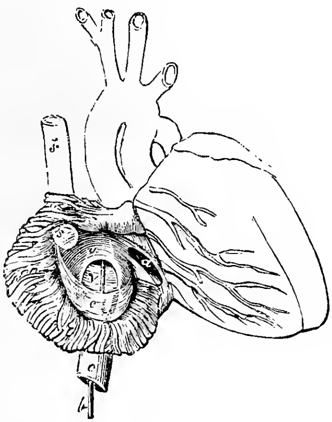


Fig. 777.

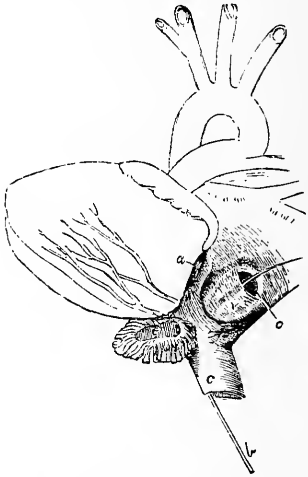


Fig. 776.—View of the front and right side of the fœtal heart, at four months, the right auricle being laid open. (From Kilian.)

a, the right auriculo-ventricular opening; *b*, a probe passed up the vena cava inferior and through the fossa ovalis and foramen ovale into the left auricle; *c*, vena cava inferior; *e*, Eustachian valve; *v*, valve of the foramen ovale; *s*, *s′*, vena cava superior.

Fig. 777.—View of the posterior and left surface of the heart of a fœtus of four months, the left auricle being opened. (From Kilian.)

a, left auricular-ventricular orifice; *c*, inferior vena cava, through which a probe *b*, is passed from below, and thence by the foramen ovale into the left auricle; *c*, left auricular appendage laid open; *o*, valve of the foramen ovale seen to be attached to the left side of the annulus ovalis of the septum.

internal division of the cavity does not take place till some time later, as on the fifth and sixth days in the chick, and in the eighth week in the human embryo. The auricular septum commences as an internal fold proceeding from the anterior wall of the common cavity, and starting from the septum of the ventricles, it grows backwards towards the entrance of the common vein or sinus, but stops short of it some distance. For a time, therefore, the veins enter the back part of the common auricular cavity. It is proper to explain, however, that, by the time at which the auricular septum is forming, the venous sinus has been modified so as to produce three veins entering the auricle at its back

part. Of these, two correspond to the permanent right superior and the inferior cava veins, and the third to a left superior cava connected with what afterwards becomes the coronary sinus. For a time, all the three vessels open so as to communicate freely with the whole auricular cavity. But changes now occur which cause the left superior cava and the inferior cava to be directed towards the left side, while the right superior cava is placed more immediately in connection with the right part of the auricular cavity.

The auricular septum, in extending itself backwards, is not completed, but leaves an oval deficiency in its lower and middle part, as the *foramen ovale*, and the inferior cava opens immediately behind this aperture. Some time later, or in the human embryo in the course of the tenth or eleventh week, two new folds make their appearance in the auricles posteriorly. One of these, constituting the *Eustachian valve*, of a crescentic form, is placed to the right of the entrance of the inferior vena cava, and in the angle between it and the orifice of the left superior cava (or great coronary sinus). This fold, besides separating these two veins, and thus throwing the opening of the left superior cava into exclusive communication with the right auricle, runs forward into the annulus ovalis or border of the anterior auricular septum, deepening the entrance of the inferior cava into a groove close to the foramen ovale, and thus directing the blood entering by that vessel through the foramen into the left auricle. (Kilian, 237).

The other fold referred to advances from the posterior wall of the common auricle to meet the anterior auricular septum, but to the left of the border of the foramen ovale. To this border, however, it adheres as it grows forwards, and thus gradually fills up the floor of the fossa ovalis. Up to the middle of fœtal life, this posterior septum being incomplete, there is a direct passage from right to left through the foramen; but, after that period, the fold in question, having advanced beyond the anterior border of the annulus ovalis and lying to the left, does not adhere to this or the fore part of the annulus, but leaves a passage between, and appears as a crescentic fold in the left auricle, which, as it passes beyond the annulus, constitutes in the last three or four months a very perfect valve against the return of blood from the left into the right auricle.

Division of the Arterial Bulb.—The third important change occurring in the heart belongs to the arterial bulb, by which there are developed from this tube the first parts or main stems of the pulmonary artery and the aorta. Within the thick walls of this arterial tube there is at first only a single subcylindrical cavity, continued from the originally single ventricle; but, soon after the partition of the ventricular cavity has commenced, or in the human embryo of the seventh week, a division of the bulb by an independent process begins to take place. This consists in the projection inwards from the distal end of the bulb of a fold of the wall, involving at first only the inner and middle coats, not perceptible externally, and advancing more rapidly on the two sides than in the middle. The cavity of the bulb is thus divided into two channels, which may be described as respectively anterior and posterior, but which, from the spiral direction taken by the folds, are somewhat twisted on each other, so that the channel which at the ventricular end is placed anteriorly becomes connected with the right ventricle and forms the pulmonary stem, and that which is placed posteriorly becomes

connected with the left ventricle and forms the commencement of the aorta. In the distal portion of the bulb, however, the pulmonary channel is situated to the left and posteriorly, and the aortic channel is to the right and most forwards; and at this end these channels are respectively connected with different aortic arches, giving rise to the permanent pulmonic and systemic vessels in the manner afterwards described. (Tonge, No. 248).

It is further to be noted that the partition of the bulb begins at the remote extremity between the fourth and fifth aortic arches, and advances towards the ventricles. There is a time, therefore, during which the ventricular septum, and the septum of the bulb, advancing towards each other, are incomplete and disunited; and from the difference in their general direction it is obvious that the septum of the bulb must be twisted upon itself, in order that it may finally unite and become continuous with that of the ventricles.

The completion of the partition of the aortic and pulmonary stems is afterwards effected by the progress of the division from within outwards through the external walls of the tubes; but the two vessels still remain united externally by a common envelope of pericardium.

The remarkable cases sometimes observed of abnormal transposition of the two great arterial stems from their natural connection with their respective ventricles may be explained by reference to the history of the development of the parts of the heart before given.

Formation of the Valves.—The formation of the auriculo-ventricular and semilunar valves takes place in the course of the second and third months in the human embryo. The semilunar valves of the aorta and pulmonary artery are formed simultaneously; and according to Tonge's observations in the chick, the plates or projections of the endocardiac lining which give rise to the valves are already formed before the septum of the bulb has reached the ventricle, and they arise at some distance from the ventricular orifices. The ventral and dorsal valves are the first to appear. Kölliker has observed these valves in the course of formation in the human embryo of seven weeks. The segments are at first of unequal size, one being much shorter than the other two. The sinuses are much later in being formed.

The auriculo-ventricular valves have been shown by the observations of Gegenbaur (No. 39), Bernays (No. 250), and Kölliker (No. 28, i.), to be formed out of plates which are originally part of the inner wall of the ventricles and auriculo-ventricular orifices. In connection with this it may be mentioned that the whole wall of the ventricles is in the earlier condition of the human heart, as in that of all animals, of a remarkable spongy or reticulated structure—a condition which remains persistent throughout life in most of the animals belonging to the three lower vertebrate classes; but in birds and mammals the reticulated structure is gradually lost by the solidification of the wall advancing from the outside inwards, and the columnæ carneæ and musculi papillares may be regarded as the vestiges of the reticulation internally.

The inner plates from which the auriculo-ventricular valves are formed contain at first a considerable amount of muscular substance, which afterwards in a great measure disappears.

In the latter changes, by which the inner plates are moulded into the form and structure of the valvular flaps, the upper or auricular part becomes fibrous, compact, and entire; the lower or ventricular part breaks up into the papillæ, which retain their muscularity and their attachment to the wall of the ventricles; while the intervening portion is more completely divided to form the thinner chordæ tendineæ in which the muscular structure is in a great measure or entirely lost. The division of the whole plates into the larger segments of the valves accompanies these changes.

The manner in which the pulmonary veins, which are formed separately in the lungs, come to be connected with the left auricle has not yet been ascertained.

No further important changes occur in the internal structure of the heart, but there are some which affect the external form and thickness of its walls. In early fœtal life the size of the heart bears a considerably greater proportion to that of the body than at a later period. At birth it is still proportionally large. For some time the auricular portion remains more voluminous than the ventricular, but in the latter half of fœtal life the permanent proportion is more nearly established. The walls of both ventricles are also thicker than in after life, and it is especially deserving of notice that the wall of the right is, up to near the time of birth, quite as thick as that of the left—a peculiarity which may be connected with the office of the right ventricle to propel the blood of the fœtus through the extended course of the ductus arteriosus, the descending aorta and the placental circulation.

II. DEVELOPMENT OF THE BLOOD-VESSELS.

The Principal Arteries. The Aorta.—The most interesting part of this history is that relating to the development of the aorta and the larger vessels arising from it.

In all vertebrates the arterial vessels proceeding from the ventral aortic bulb of the heart form five (and in some more) pairs of arches surrounding the anterior or pharyngeal part of the alimentary canal, and after a certain progress in development, uniting dorsally into the roots of the aorta of the trunk. At first, however, there is only one pair of these arches, and these are continued separately into the two vessels which represent the primitive state of the aorta.

It was first suggested by Serres, and subsequently proved by the writer of this chapter, by means of sections (No. 230, 1831), that the main aorta is formed by the median fusion of the two vessels previously separate. This fusion begins in the chick about the fortieth hour in the middle of the dorsal region, and extends forwards till it reaches the roots of the branchial arches, and backwards as far ultimately as the division into the iliac arteries. When this union reaches the place where the vitelline arteries pass out on each side, these vessels, each of which was previously the continuation merely of one of the primary main arteries, appear now as branches of a single and median aorta. The iliac are the next large vessels formed from the hinder part of the aorta. The first vessels belonging to these trunks are not, however, those of the lower limbs, for these do not yet exist; but rather the umbilical or hypogastric arteries, developed at a very early period in connection with the allantois, and subsequently attaining to a large size along with the growth of the placenta. As the limbs are formed, the arteries are developed in them which afterwards become the iliac divisions of the main aorta; but they are for a long time comparatively small, while the umbilical arteries are of very large size, so that, even up to the conclusion of fœtal life, these last appear to form the principal part of the two large vessels into which the aorta divides.

The relation of the process of mesial fusion of the originally double aorta to the occurrence of a permanent double canal in that vessel as a malformation,

described by Vrolik, Schröder van der Kolk, and Cruveilhier, and observed also by Allen Thomson, has already been referred to in vol. i., p. 350.

According to Serres, the vertebral arteries within the cranium are originally separate, and the basilar artery results from their mesial union or fusion in the same manner as occurs in the aorta; and the union of the two anterior cere-

Fig. 778.

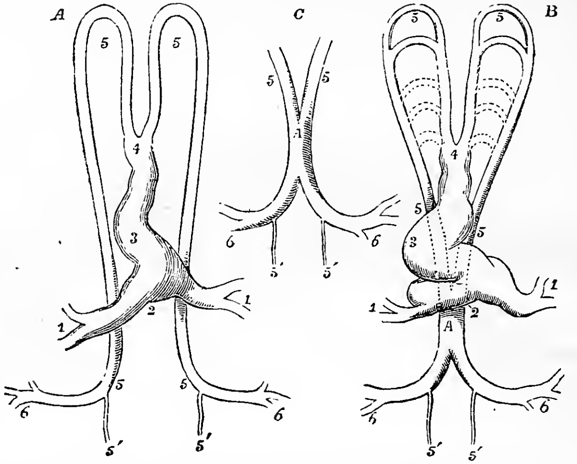


Fig. 778.—Diagrammatic outlines of the heart and primitive vessels of the embryo chick as seen from below and enlarged. (A. T.)

A, soon after the first establishment of the circulation; B, C, at a somewhat later period; 1, 1, the veins returning from the vascular area; 2, 3, 4, the heart, now in the form of a notched tube; 5, 5 (upper), the two primitive aortic arches; 5, 5 (lower), the primitive double aorta; A, the single or united aorta; 5′, 5′, the continuation of the double aortæ beyond the origin of the large omphalo-mesenteric arteries, 6, 6. The division above 4 is represented as carried rather too far down.

bral arteries in the forepart of the circle of Willis is another example of the same process. It seems probable that the internal cross band observed by John Davy in the interior of the basilar artery may be a remnant of the septum or united walls of the two vertebral arteries.

Aortic or Branchial Arches.—The two primitive arterial arches which lead into the dorsal aorta from the arterial bulb of the rudimentary heart, at the time of the establishment of the first circulation, are the most anterior of a series of five pairs of vascular arches which are developed in succession round this part of the pharynx; and which, since their discovery by Rathke in 1825 (No. 173), have been regarded with much interest, as corresponding with those which are the seat of development of the subdivided blood-vessels of the gills in fishes and amphibia. These vascular arches thus exhibit in the amniota, along with the branchial clefts and visceral arches, a typical resemblance to the structure of gills; and although no full development of these respiratory organs occurs in such animals, they give rise by their various transformations to the permanent pulmonary and aortic stems and the principal vessels which spring from them.

The form and position of the primitive aortic arches, up to the time of their transformation into permanent vessels, or their disappearance, are nearly the same in reptiles, birds, and mammals; and the main

differences in the seat and distribution of the large permanent vessels are to be traced to changes in the patency and extent of growth of the several arches. The five pairs of arches do not all co-exist at the same time, for they are developed in succession from before backwards; and by the third day of incubation, or by the corresponding period of the fourth week in the human embryo, when the posterior arches have been formed, already the two anterior arches, beginning with the first one, have become partially obliterated. Each of the first four branchial

Fig. 779.

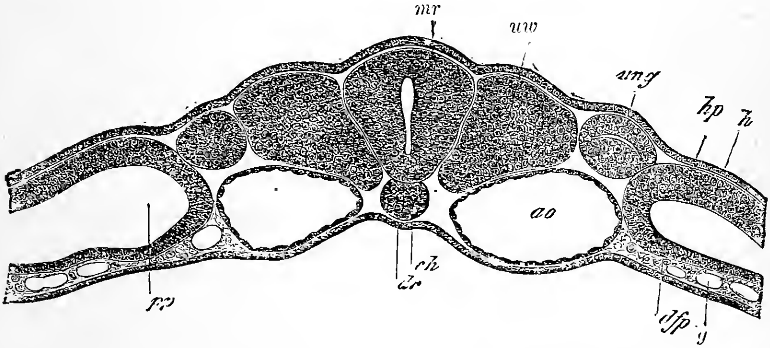


Fig. 779.—Transverse section of an embryo rabbit, of nine days and two hours, in the middle dorsal region. $\frac{158}{1}$. (From Kölliker.)

mr, medullary tube; *uw*, protovertebral mass; *h*, epiblast; *hp*, parietal mesoblast; *dfp*, visceral division of the mesoblast; *pp*, pleuro-peritoneal cavity between them; *ung*, primitive segmental duct; *g*, vessels in the visceral mesoblast; *ch*, notochord; *dr*, intestinal groove of the hypoblast.

arches occupies a place in the substance of the visceral arches, and in front of one of the pharyngeal clefts. The first or anterior is therefore situated in the mandibular arch, and in front of the tympano-Eustachian or hyomandibular cleft; and the fifth arterial arch is placed behind the fourth pharyngeal cleft and in the substance of the neck, in which there is no distinct arch in the higher animals, but which is the seat of a developed branchial bar in some aquatic vertebrates.

The vessels forming the arterial arches are given off on each side in succession from two short canals, into which the primitive arterial bulb divides immediately in front of the place where it joins the neck. These may be named the ventral or anterior aortic roots; and similarly, when they have passed round the wall of the pharynx, the branchial arches unite in succession into a vessel on each side, thus forming the dorsal or posterior aortic roots.

On the third and fourth days in the chick, and from the fourth to the sixth week in the human embryo, there are still three complete pairs of arterial arches passing round the pharynx, and connected both before and behind with the anterior and posterior aortic roots previously mentioned. The transformations of these arches were in part traced by Von Baer and various other observers, but the fuller knowledge of their changes is due to the later researches of Rathke (No. 240, iv); and although some points are still left in doubt, their history may now be given from these observations, which receive interesting illustration from the investigation

of the various examples of congenital malformation, the greater number of which are manifestly related to variations in the natural mode of development (see Fig. 780).

From these researches it appears that the permanent vessels owe their formation to the persistence of certain of the fœtal arches or parts of them, while other arches or portions of them become obliterated and disappear. Thus it is ascertained that in mammals the main aortic arch, which in the adult passes to

Fig. 780.

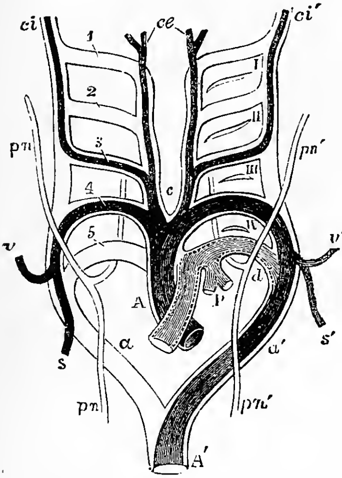


Fig. 780.—Diagram of the aortic or branchial vascular arches of the mammal, with their transformations giving rise to the permanent arterial vessels. (After Rathke, slightly altered.)

A, P, primitive arterial stem or aortic bulb, now divided into A, the ascending part of the aortic arch, and P, the pulmonary; *a*, the right; *a′*, the left aortic root; A′, the descending aorta. On the right side, 1, 2, 3, 4, 5 indicate the five primitive arterial arches; on the left side, I, II, III, IV the four pharyngeal clefts, which, for the sake of clearness, have been omitted on the right side. It will be observed, that while the fourth and fifth pairs of arches rise from the part of the aortic bulb or stem, which is at first undivided, the first, second, and third pairs are branches above *c*, of a secondary stem on each side. The permanent systemic vessels are represented in deep shade, the pulmonary arteries lighter; the parts of the primitive arches which have only a temporary existence are drawn in outline only. *c*, placed between the permanent common carotid arteries; *ce*, the external carotid arteries; *ci*, *ci′*, the right and left internal carotid arteries; *s*, the right subclavian rising from the right aortic root beyond the fifth arch; *v*, the right vertebral from the same opposite the fourth arch; *v′*, *s′*, the left vertebral and subclavian arteries rising together from the left or permanent aortic root opposite the fourth arch; P, the pulmonary arteries rising together from the left fifth arch; *d*, the outer or back part of the left fifth arch, forming the ductus arteriosus; *pn*, *pn′*, the right and left pneumogastric nerves, descending in front of the aortic arches, with their recurrent branches represented diagrammatically as passing behind, with a view to illustrate the relations of these nerves respectively to the right subclavian artery (4) and the arch of the aorta and ductus arteriosus (*d*).

the left of the trachea and gullet, is formed by the persistence of the fourth embryonic arterial arch of the left side, which not only remains patent, and is connected with the aortic stem of the arterial bulb, but by the increase of its width and the thickness of its walls keeps pace in its rate of growth with that of other parts of the body, so that it soon surpasses all the rest of the arches in its dimensions. In birds, however, the permanent aortic arch is on the right of the trachea and gullet, being formed by the persistence of the fourth embryonic arch of the right side; while, in all reptiles, as there are two permanent aortic arches, it is by the persistence of both the right and left fourth arches that the two aortas are produced, the right being that which is most directly connected with the systemic or left ventricle.

The pulmonary arteries of mammals would appear from Rathke's observations to be developed in connection with only one fœtal arterial arch—viz., the fifth of the left side—from the middle part of which they are formed as branches, and the whole fifth arch of the right side after a time undergoes atrophy and obliteration. The first part of the left fifth arch, becoming the common pulmonary artery, is

connected with that division of the arterial bulb which is separated as the pulmonary stem; but the remote part of this arch also remains fully patent, and undergoing development equally with the rest of its extent, continues to lead into the *left* root of the aorta as ductus arteriosus Botalli, which serves to convey the blood from the right ventricle of the fœtal heart into the descending aorta, but becomes obliterated at the time of birth.

This duct is therefore in mammals due to a persistent condition of the fifth left branchial arch; but, in birds and reptiles, the process of transformation is somewhat different, for in them the right and left pulmonary arteries (excepting in those serpents in which there is only one lung developed) are formed in connection with the respective right and left fifth branchial arches, and there are thus two ductus arteriosi during fœtal life, the short one of the right side corresponding to that which is *left* or sinistral in mammals, and the longer one of the left side passing round the pharynx into the left aortic root. Both of these arches are obliterated at the time of the exclusion of the bird from the egg; but in some reptiles the ductus arteriosi remain permanently open during life.

The subclavian and vertebral arteries were shown by Rathke to spring from the posterior aortic roots at a place between the junction of the fourth and fifth arches. In mammals, the vessels on the left side are from the first in direct connection with the aortic root at the place which they permanently occupy; but upon the right side, as the fourth arch and the aortic root are obliterated posteriorly, the passage for blood from the aortic stem into the subclavian trunk is formed by the persistence of the forepart of the fourth right arch as far as the place where it meets the origin of the subclavian and vertebral arteries.

The common carotid trunks, occupying the region which afterwards becomes the neck, but which is at first absent or extremely short, are formed by the anterior divisions of the aortic roots; while the external carotid artery is due to the persistence of a channel in the continuation of each anterior aortic root, and the internal carotid artery arises from the persistence of the crossing third arch and the upper part of the posterior aortic root.

Thus it falls out that, in man and a certain number of mammals, an innominate artery is formed on the right side by the union of the first part of the fourth right aortic arch leading into the right subclavian with the right anterior aortic root which forms the common carotid; while, on the left side, the carotid and subclavian vessels rise separately from the permanent aortic arch in consequence of the distance between them in the original fœtal condition.

It does not come within the scope of this work to describe the further steps of development of these vessels, nor to enter into an explanation of the manner in which abnormal position of the arch of the aorta and its branches, or of the pulmonary arteries, may be supposed to arise. For further information on this subject the reader is referred to the short account of the varieties given in the description of the blood-vessels in the first volume of this work, as well as to the third volume of Henle's Handbuch, and to the special works of Tiedemann and Richard Quain on the arteries.

THE GREAT VEINS.

In the early embryo, before the development of the allantois, a right and a left vitelline (or omphalo-mesenteric) vein bring back the blood from the walls of the umbilical vesicle, and unite to form a short trunk, the meatus venosus, which is continued into the auricular extremity of the rudimentary heart.

In the first commencement of the allantoid circulation, or in the fourth week of fœtal life, two umbilical veins are seen coming from the placenta, and uniting to form a short trunk, which opens into the common vitelline vein. Very soon the right vitelline vein and right umbilical vein disappear. In connection with the common trunk of these veins, proceeding to the liver, two sets of vessels make their appearance in the early stage of its growth. Those furthest from the heart, named *venæ hepaticæ advehentes*, become the right and left divisions of the portal vein; the others are the hepatic veins, *venæ hepaticæ revehentes.* The portion of vessel intervening between those two sets of veins

forms the *ductus venosus*, and the part above the hepatic vein, being subsequently joined by the ascending vena cava, forms the upper extremity of that vein. Into the remaining or left vitelline vein there open the mesenteric and splenic veins. The part above the latter forms the trunk of the portal vein; and the portion

Fig. 781.

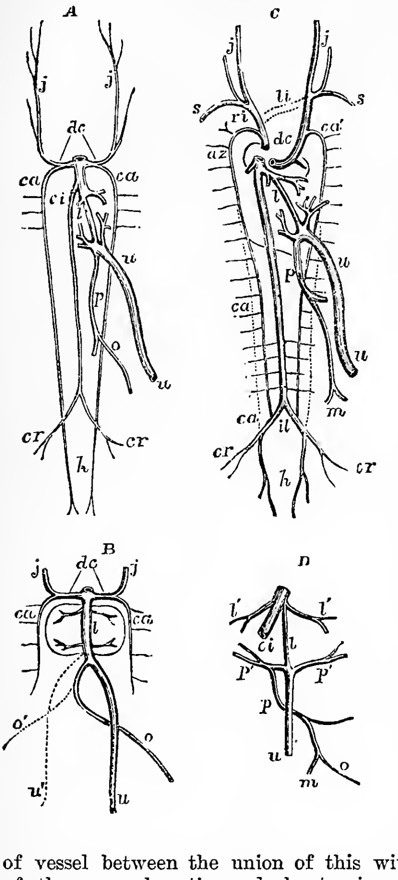


Fig. 781.—Diagrams illustrating the development of the great veins. (After Kölliker.)

A, plan of the principal veins of the fœtus of about four weeks, or soon after the first formation of the vessels of the liver and the vena cava inferior.

B, veins of the liver at a somewhat earlier period.

C, principal veins of the fœtus after the establishment of the placental circulation.

D, veins of the liver at the same period.

dc, the right and left ducts of Cuvier; *ca*, the right and left cardinal veins; *j*, *j*, the jugular veins; *s*, the subclavian veins; *az*, the azygos vein; *u*, the umbilical or left umbilical vein; *u'*, in B, the temporary right umbilical vein; *o*, the vitelline vein; *o'*, the right; *m*, the mesenteric veins; *p*, the portal vein; *P'*, *P'*, the venæ advehentes; *l*, the ductus venosus; *l'*, *l'*, the hepatic veins; *ci*, vena cava inferior; *il*, the division of the vena cava inferior into common iliac veins; *cr*, the external iliac or crural veins; *h*, the hypogastric or internal iliac veins, in the line of continuation of the primitive cardinal veins.

In C, *li*, in dotted lines, the transverse branch of communication between the jugular veins which forms the left brachio-cephalic vein; *ri*, the right brachio-cephalic vein; *ca'*, the remains of the left cardinal vein by which the superior intercostal veins fall into the left brachio-cephalic vein; above *P*, the obliquely crossing vein by which the hemiazygos joins the azygos vein.

of vessel between the union of this with the umbilical vein and the origin of the venæ hepaticæ advehentes is so altered that the portal trunk opens into the commencement of the right vena advehens.

At the time of the commencement of the placental circulation, two short transverse venous trunks, the *ducts of Cuvier*, open, one on each side, into the auricle of the heart. Each is formed by the union of a superior and an inferior vein, named respectively the *primitive jugular* and the *cardinal.*

The *primitive jugular* vein receives the blood from the cranial cavity by channels in front of the ear, which are subsequently obliterated: in the greater part of its extent it becomes the internal jugular vein; and near its lower end it receives small branches, which grow to be the external jugular and subclavian veins. The *cardinal veins* are the primitive vessels which return the blood from the Wolffian bodies, the vertebral column, and the parietes of the trunk. The inferior vena cava is a vessel of later development, which opens into the trunk of the umbilical and vitelline veins, above the venæ hepaticæ revehentes. The iliac veins, which unite to form the inferior vena cava, communi-

cate with the cardinal veins. The inferior extremities of the cardinal veins are persistent as the internal iliac veins. Above the iliac veins the cardinal veins are obliterated in a considerable part of their course; their upper portions then become continuous with two new vessels, the *posterior vertebral veins* of Rathke, which receive the lumbar and intercostal twigs.

As development proceeds, the direction of the ducts of Cuvier is altered by the

Fig. 782.

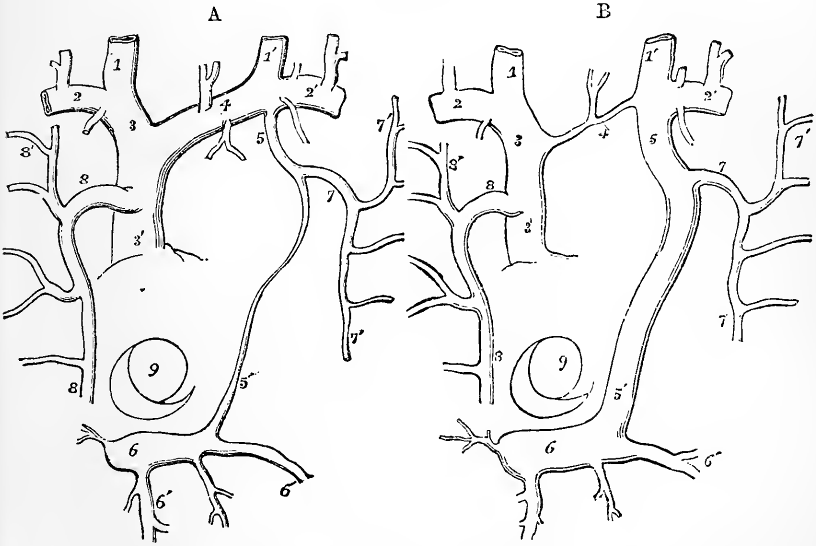


Fig. 782.—A and B.—Diagrammatic outlines of the vestige of the left superior cava and of a case of its persistence. (Sketched after Marshall.) $\frac{1}{2}$.

A, brachio-cephalic veins with the superior intercostal, azygos, and principal cardiac veins. (In this and in B the veins are supposed to be seen from before.)

B, the same in a case of persistence of the left superior cava, showing its communication with the sinus of the coronary vein. The views are supposed to be from before, the parts of the heart being removed or seen through.

1, 1′, the internal jugular veins; 2, 2′, subclavian veins; 3, right innominate; 3′, right or regular superior cava; 4, in A, the left innominate; in B, the transverse or communicating vein between the right and left superior venæ cavæ; 5, in A, the opening of the superior intercostal vein into the innominate; 5′, vestige of the left superior cava or duct of Cuvier; 5, 5′, in B, the left vena cava superior abnormally persistent, along with a contracted condition of 4, the communicating vein; 6, the sinus of the coronary vein; 6′, branches of the coronary veins; 7, the superior intercostal trunk of the left side, or left cardinal vein; 8, the principal azygos or right cardinal vein; 7′, 8′, some of the upper intercostal veins; 9, the opening of the inferior vena cava, with the Eustachian valve.

descent of the heart from the cervical into the thoracic region, and becomes the same as that of the primitive jugular veins. A communicating branch makes its appearance, directed transversely from the junction of the left subclavian and jugular veins, obliquely across the middle line to the right jugular; and further down in the dorsal region between the posterior vertebral veins a communicating branch passes obliquely across the middle line from right to left. The communicating branch between the primitive jugular veins is converted into the left brachio-cephalic or innominate vein. The portion of vessel between the right subclavian vein and the termination of the communicating branch becomes the right brachio-cephalic vein. The portion of the primitive jugular vein below the communicating vein, together with the right duct of Cuvier, forms

the vena cava superior, while the cardinal vein opening into it is the extremity of the great vena azygos. On the left side, the portion of the primitive jugular vein placed below the communicating branch, and the cardinal and posterior vertebral veins, together with the cross branch between the two posterior vertebral veins, are converted into the left superior intercostal and left superior and inferior azygos veins. The variability in the adult arrangement of these vessels depends on the

Fig. 783.

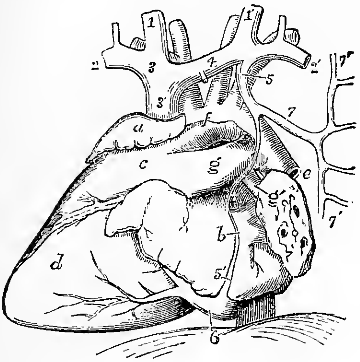


Fig. 783.—View of the fœtal heart and great vessels, from the left side, to show the vestige of the left superior cava vein in situ. (This figure is planned after one of Marshall's, and slightly altered according to an original dissection.)

a, right auricle; *b*, left auricle and pulmonary veins; *c*, the conus arteriosus of the right ventricle; *d*, the left ventricle; *e*, descending aorta; +, vestigial fold of the pericardium; *f*, arch of the aorta, with a part of the pericardium remaining superiorly; *g*, main pulmonary artery and ductus arteriosus; *g'*, left pulmonary artery; 1, 1', right and left internal jugular veins; 2, 2', subclavian veins; 3, 3', right innominate and superior vena cava; 4, left innominate or communicating vein; 5, 5', remains of the left superior cava and duct of Cuvier, passing at + in the vestigial fold of the pericardium, joining the coronary sinus, 6, below, and receiving above the superior intercostal vein, 7; 7', 7', the upper and lower intercostal vein, joining into one.

different extent to which the originally continuous vessels are developed or atrophied at one point or another. The left duct of Cuvier is obliterated, except at its lower end, which always remains pervious as the coronary sinus. But even in the adult, traces of this vessel can always be recognised in the form of a fibrous band, or sometimes a narrow vein, which descends obliquely over the left auricle; and in front of the root of the left lung there remains a small fold of the serous membrane of the pericardium, the *vestigial fold*, so named by Marshall, to whom is due the first full elucidation of the nature and relations of the left primitive vena cava superior (No. 253).

The left duct of Cuvier has been observed persistent as a small vessel in the adult. Less frequently a right and a left innominate vein open separately into the right auricle, an arrangement which is also met with in birds and in certain mammals, and which results from the vessels of the left side being developed similarly to those of the right, while the cross branch remains small or absent (Quain, No. 243).

A case is recorded by Gruber (No. 254) in which the left vena azygos opened into the coronary sinus, and was met by a small vein descending from the union of the subclavian and jugular. Here, then, the jugular veins had been developed in the usual manner, while the left vena azygos continued to pour its blood into the duct of Cuvier.

III. PECULIARITIES OF THE FŒTAL ORGANS OF CIRCULATION.

It may be useful here to recapitulate shortly the peculiarities of structure existing in the advanced stage of the formation of the fœtal organs of circulation, with reference to their influence in determining the course of the blood during intra-uterine life, and the changes which occur in them upon the establishment of pulmonary respiration at birth.

1. The **foramen ovale** retains the form of a free oval opening in the septum auricularum up to the fourth month, but in the course of that month and the next the growth of the *valvular plate* or curtain, which fills up the floor of the fossa

ovalis, becomes complete, so that in the last three and a half months the blood can only pass from the right into the left auricle, but not in a contrary direction.

2. The **Eustachian Valve** constitutes a crescentic fold of the lining structure of the heart, which is so situated as to direct the blood entering the auricle by the inferior cava towards the opening of the foramen ovale.

Fig. 784.

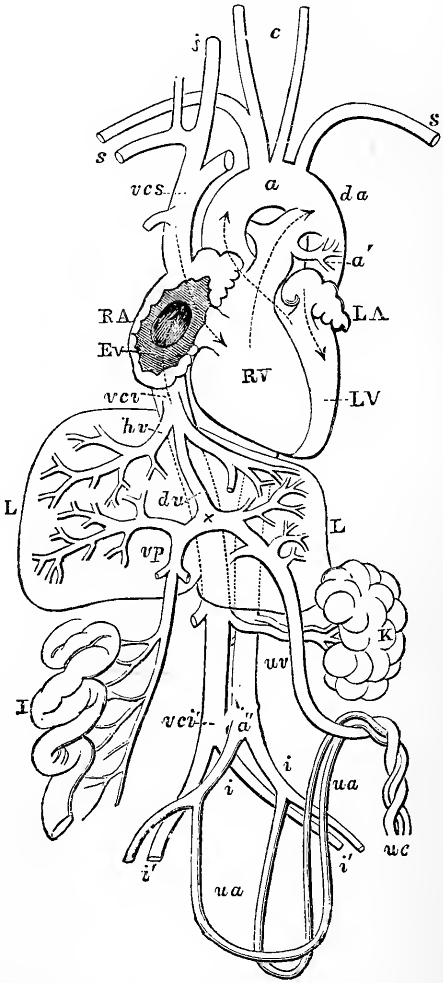


Fig. 784.—Diagrammatic outline of the organs of circulation in the fœtus of six months. (A. T.)

RA, right auricle of the heart; RV, right ventricle; LA, left auricle; Ev, eustachian valve; LV, left ventricle; L, liver; K, left kidney; I, portion of small intestine; *a*, arch of the aorta; *a'*, its dorsal part; *a''*, lower end; *vcs*, superior vena cava; *vci*, inferior vena where it joins the right auricle; *vci'*, its lower end; *s*, subclavian vessels; *j*, right jugular vein; *c*, common carotid arteries; four curved dotted arrow lines are carried through the aortic and pulmonary opening, and the auriculo-ventricular orifices; *da*, opposite to the one passing through the pulmonary artery, marks the place of the ductus arteriosus; a similar arrow line is shown passing from the vena cava inferior through the fossa ovalis of the right auricle, and the foramen ovale into the left auricle; *hv*, the hepatic veins; *vp*, vena portæ; *x* to *vci*, the ductus venosus; *uv*, the umbilical vein; *ua*, umbilical arteries; *uc*, umbilical cord cut short; *i i'*, iliac vessels.

3. The **ductus arteriosus** establishes a communication between the main pulmonary artery and the aorta, by which the blood from the right ventricle is carried mainly into the dorsal aorta.

4. **Umbilical Vessels.**—The two large hypogastric or *umbilical arteries*, prolonged from the iliac arteries, passing out of the body of the fœtus, proceed along the umbilical cord, to be distributed in the fœtal portion of the placenta. From the placenta the blood is returned by the umbilical vein, which, after entering the abdomen, communicates by one branch with the portal vein of the liver, and is continued by another, named *ductus venosus*, into one of the hepatic veins, through which it joins the main stem of the vena cava inferior.

Course of the Blood in the Fœtus.—The right auricle of the fœtal heart receives blood from the two venæ cavæ and the coronary vein. The blood brought by the superior cava is simply the venous blood returned from the head

and upper half of the body; whilst the inferior cava, which is considerably larger than the superior, conveys not only the blood from the lower half of the body, but also that which is returned from the placenta and from the liver. This latter stream of blood reaches the vena cava inferior, partly by a direct passage—the *ductus venosus*—and partly by the hepatic veins, which bring to the vena cava inferior all the blood circulating through the liver, whether derived from the supply of placental blood entering that organ by the umbilical vein, or proceeding from the vena portæ or hepatic artery.

The blood of the superior vena cava, passing from the right auricle into the right ventricle, is thence propelled into the trunk of the pulmonary artery. A small part of it is distributed through the branches of that vessel to the lungs, and returns by the pulmonary veins to the left auricle; but, as these vessels remain comparatively undilated up to the time of birth, by far the larger part passes through the ductus arteriosus into the dorsal aorta, and is thence distributed in part to the lower half of the body and the viscera, and in part is conveyed along the umbilical arteries to the placenta. From these several organs it is returned by the vena cava inferior, the venæ portæ, and the umbilical vein; and, as already noticed, reaches the right auricle through the trunk of the inferior cava.

Of the blood entering the heart by the inferior vena cava, only a small part is mingled with that of the superior cava, so as to pass into the right ventricle; by far the larger portion, directed by the Eustachian valve through the foramen ovale, flows into the left auricle, and thence, together with the small quantity of blood returned from the lungs by the pulmonary veins, passes into the left ventricle, from whence it is sent into the arch of the aorta, to be distributed almost entirely to the head and upper limbs.

Sabatier was the first to call attention particularly to the action of the Eustachian valve in separating the currents of blood entering the right auricle by the superior and inferior venæ cavæ (No. 236). This separation, as well as that occurring between the currents passing through the aortic arch and the ductus arteriosus into the descending aorta, was illustrated experimentally by John Reid (No. 241). A striking confirmation of the extent to which the last mentioned division of the two currents of the fœtal blood may take place, without disturbance of the circulation up to the time of birth, is afforded by the examples of malformation in which a complete obliteration has existed in the aortic trunk immediately before the place of the union of the ductus arteriosus with the posterior part of the aortic arch.

CHANGES IN THE CIRCULATION AT BIRTH.

The changes which occur in the organs of circulation and respiration at birth, and which lead to the establishment of their permanent condition, are more immediately determined by the inflation of the lungs with air in the first respiration, the accompanying rapid dilatation of the pulmonary blood-vessels with a greater quantity of blood, and the interruption to the passage of blood through the placental circulation. These changes are speedily followed by shrinking and obliteration of the ductus arteriosus, in the space between the division of the right and left pulmonary arteries and its junction with the aorta, and of the umbilical arteries from the hypogastric trunk to the place of their issue from the body by the umbilical cord; by the cessation of the passage of blood through the foramen ovale, and somewhat later by the closure of that foramen, and by the obliteration of the umbilical vein as far as its entrance into the liver, and of the ductus venosus within that organ.

The process of obliteration of the arteries appears to depend at first mainly on the contraction of their coats, but this is very soon followed by a considerable thickening of their substance, reducing rapidly their internal passage to a narrow tube, and leading in a short time to final closure, even although the vessel may not present externally any considerable diminution of its diameter. It commences at birth, and is perceptible after a few respirations have occurred. It makes rapid progress in the first and second days, and by the third or fourth day the passage through the umbilical arteries is usually completely interrupted.

The ductus arteriosus is rarely found open after the eighth or tenth day, and by three weeks it has in almost all instances become completely impervious.

The process of closure in the veins is slower, there not being the same thickening or contraction of their coats; but they remain empty of blood and collapsed, and by the sixth or seventh day are generally closed.

Although blood ceases at once to pass through the foramen ovale from the moment of birth, or as soon as the left auricle becomes filled with the blood returning from the lungs, and the pressure within the two auricles is equalised, yet the actual closure of the foramen is more tardy than any of the other changes now referred to. It is gradually effected by the union of the forepart of the valvular fold forming the floor of the fossa ovalis with the margin of the annulus on the left side; but the crescentic margin is generally perceptible in the left auricle as a free border beyond the place of union, and not unfrequently the union remains incomplete, so that a probe may be passed through the reduced aperture. In many cases a wider aperture remains for more or less of the first year of infancy, and in certain instances there is such a failure of the union of the valve as to allow of the continued passage of venous blood, especially when the circulation is disturbed by over-exertion, from the right to the left auricle, as occurs in the malformation attending the morbus cœruleus.

LYMPHATIC SYSTEM.

Closely connected with the blood-vascular system, and also arising from the mesoblast, are the less conspicuous and sometimes rather indefinite components of the lymphatic system, consisting of the lymphatic vessels, glands, and the lymph spaces, the histological development of which has been referred to in the first part of this volume (p. 208).

Like the bloodvessels, the lymphatic vessels are intimately associated with the connective tissue, and they take their origin in a somewhat similar manner in spaces which are formed in the primitive blastema. It is also an interesting fact that these vessels are in frequent communication with the intermesoblastic space or pleuro-peritoneal cavity.

All the lymphatic vessels are at first similar to capillary bloodvessels, being lined only by flat epithelium; and many of them, though of some size, do not pass beyond this stage, while others acquire fibrous, contractile, and adventitious coats in a manner exactly the same as do the arteries or veins.

The lymphatic glands consist at first of networks of lymphatic vessels and spaces having numerous lymph cells produced within them; but later they have added to them connective tissue elements and bloodvessels in considerable quantity.

The Spleen.—There is perhaps none of the organs which have been ranked as vascular glands which so well deserves the name as the spleen, for it appears to be closely associated with both the lymphatic and the blood-vascular systems. It is not formed at a very early stage of development, but begins to appear in the human embryo in the latter half of the second month. It is developed in the substance of the mesogastrium, and is at first in close connection with the pancreas, but without any hypoblastic evolution, and proceeding entirely from mesoblast, apparently from the same mass as that in which the pancreas takes its origin (W. Müller, No. 256). Its progress is not rapid: it acquires vessels and trabecular fibres in the third month, and there is a large increase of the cells of the pulp; but the Malpighian corpuscles are only formed later, and are not distinctly seen till near the end of fœtal life. For the development of the Thyroid and Thymus Glands see p. 889.

IV. DEVELOPMENT OF THE ALIMENTARY CANAL AND ASSOCIATED ORGANS.

The parts of the body of which the development has been previously described all take their origin from either or both of the upper and middle layers of the blastoderm. Those which are now to be considered proceed, in the first instance, from the inflections and growth of the hypoblast or lower layer, with which, however, there are combined, in almost all of the organs, elements which are derived from the visceral layer of the mesoblast. These organs consist of the alimentary canal, with its integral and accessory glands, such as the liver and pancreas, the respiratory organs, the larynx, trachea, and lungs, the serous coverings of pleuræ and peritoneum, &c.

Primary Development.—Mesenteron.—The principal part of the alimentary canal is formed at first by a simple inflection of the hypoblast, and its wall then consists of no more than the epithelial cells derived from that layer of the blastoderm. In the most of its extent, however, this epithelial wall has acquired considerable thickness as compared with the part of the hypoblast external to the body of the embryo.

The primary digestive cavity of birds and mammals, as it extends from one end of the embryo to the other below the vertebral axis, and

Fig. 785.

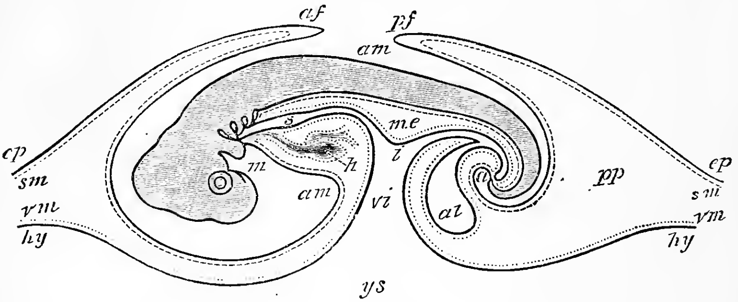


Fig. 785.—Enlarged diagrammatic outline of a longitudinal vertical section of the chick and neighbouring parts of the blastoderm on the fourth day. (A. T.)

ep, epiblast, and *sm*, somatic mesoblast, together forming the *somatic plate ; hy*, hypoblast, and *vm*, visceral mesoblast, together forming the *visceral plate ; af*, cephalic fold ; *pf*, caudal fold of the amnion ; *am*, cavity of the true amnion ; *ys*, yolk-sack, leading by the vitello-intestinal aperture to *i*, the intestine ; *s*, the stomach and pharynx ; *a*, the future anus still closed ; *m*, the buccal cavity or mouth formed in epiblast and still closed from the pharynx at the fauces, which are not shown ; *me*, the mesentery ; *al*, the allantoid vesicle communicating by its pedicle with the hinder intestine ; *pp*, the space between the outer and inner folds of the amnion, which is an extension of the body cavity or pleuro-peritoneal space within the embryo between the somatic and visceral mesoblasts. The shaded part of the figure represents the head and trunk of the embryo in which the eye and the jaws with the branchial bars and clefts are indicated. The epiblast and hypoblast are drawn with entire lines, the somatic mesoblast with an interrupted and the visceral mesoblast with a dotted line.

not including the buccal and anal portions derived from epiblastic involution, presents at first a manifest division into three parts. One of these, occupying the part of the embryo which is enclosed by the cephalic

fold, and which may be named the *foregut*, comprises the rudiments of the pharynx and gullet, the stomach and duodenum. The posterior division, which is comparatively short, occupies the caudal fold of the embryo, and corresponds mainly to the parts in the neighbourhood of the future anus, with a prolongation of the gut, which may be called post-

Fig. 786.

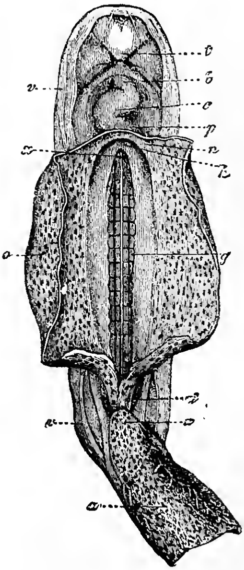


Fig. 786.—THE SAME EMBRYO AS IN FIG. 667 REMOVED FROM THE MEMBRANES, MORE HIGHLY MAGNIFIED AND SEEN FROM BELOW. (From Kölliker after Coste.)

a, allantois already forming an umbilical pedicle; *u*, urachus or stalk; *i*, hinder gut; *v*, amnion; *o*, yolk-sac; *g*, primitive aortas lying under the vertebral column, separated by the white line; *x*, wide opening of the intestine into the yolk-sac; *k*, place where the umbilical and omphalo-mesenteric veins meet and pass into the heart; *p*, pericardial cavity; *c*, heart; *h*, aorta; *t*, frontal process.

anal or sub-caudal. Both of these parts have from the first a tubular form, and are closed respectively by the inflection of the whole blastodermic layers at the anterior and posterior extremities of the body. The middle division, or that in which the greater part of the small and large intestines will afterwards be formed, has primarily the form of a long and wide groove, lying close below the vertebral bodies, and leading at its opposite ends into the cephalic and caudal portions of the gut; it is freely open throughout on its ventral aspect into the cavity of the yolk-sac, with the blastodermic walls of which, as formerly described, the constituents of the intestinal walls are directly continuous.

Foregut.—As development proceeds in the forepart of the alimentary canal, a change in its form manifests itself, by which one part, becoming dilated, forms the commencement of the stomach, while the others remain of smaller diameter as gullet and duodenum; and in connection with different parts of these the rudiments of the lungs, liver, and pancreas are first formed.

When the tubular parts of the gut have attained to some length, a change of position gradually accompanies their further development. While the œsophageal part remains comparatively straight, the dilated portion of the tube which forms the stomach turns over on its right side, so that the border which is connected to the vertebral column by the mesenteric fold (or true mesogastrium) comes to be turned to the left—the position of the tube being still vertical, like the stomach of some animals. By degrees it becomes more dilated, chiefly on what is now the left border but subsequently becomes the great curvature, and assumes more of the oblique position of the adult, carrying with it the mesogastrium, from which the great omentum is afterwards produced. A slight indication of the pylorus is seen at the third month. Upon the surface of the part of the canal which immediately succeeds the stomach, and which forms the duodenum, the rudiments of the liver, pancreas,

and spleen are simultaneously deposited, in the manner stated in the description of the development of these organs.

Midgut.—Previously to the occurrence of the changes in the foregut mentioned above, the middle open part shortens, more and more of it being converted into the tubular intestine, and at last, as before

Fig. 787.

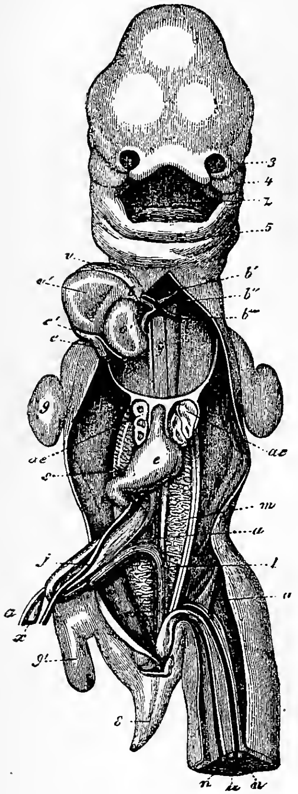


Fig. 787.—Human embryo of thirty-five days seen from before. (From Kölliker after Coste.)

3, left external nasal process; 4, superior maxillary process; 5, lower maxillary process; *z*, tongue; *b*, aortic bulb; *b′*, third aortic arch or carotid stem; *b″*, fourth or main aortic arch; *b‴*, fifth arch or ductus Botalli; *c*, the superior cava and right azygos vein; *c′*, the common venous sinus of the heart; *c″*, the common stem of the left vena cava and left azygos; *o′*, left auricle of the heart; *v*, right; *v′*, left ventricle; *a e*, lungs; *e*, stomach; *j*, left omphalo-mesenteric vein; *s*, continuation of the same behind the pylorus, which becomes afterwards the vena portæ; *x*, vitello-intestinal duct; *a*, right omphalo-mesenteric artery; *m*, Wolffian body; *i*, rectum; *n*, umbilical artery; *u*, umbilical vein; 8, tail; 9, anterior; 9′, posterior limb. The liver has been removed.

explained, there remains only the narrow opening by which the gradually lengthening ductus vitello-intestinalis leads into the umbilical vesicle. The middle part of the intestinal canal has, when first produced, more or less the form of a straight tube lying close to the vertebral column; but, as soon as it increases in length, it is thrown into the shape of a loop bent downwards to the umbilicus—a change which is preceded and accompanied by the formation of the mesentery. The latter structure is undoubtedly entirely due to a proliferation and median union of mesoblastic elements, which, extending themselves between the mesoblast surrounding the notochord and the elongating gut, become developed into the vascular and other parts of the mesentery, as was long ago shown by Von Baer. The mesentery thus forms a mesial partition extending between the gut and the dorsal wall of the embryo, at first quite simple, but afterwards elongating, and becoming more complicated in proportion to the development of the intestinal tube. The mesoblast also, by its visceral division, furnishes the contractile, vascular, and connective tissue elements of the intestinal walls. The extent to which the glandular elements of the alimentary canal are supplied by the hypoblast, to which their origin was entirely attributed by Remak, or furnished rather by mesoblast from the protovertebral mass, as held by Schenk, is not yet fully determined.

The place of transition from the small to the large intestine, which

is soon indicated by the protrusion of the cæcum, is at a point just behind the apex or middle of the simple loop already mentioned as existing after the first elongation of the tubular gut. As the *small* intestine grows, the part behind the duodenum forms coils, some of which at first lie in a dilatation of the commencing umbilical cord (see fig. 789), but retire again into the abdomen about the twelfth week; afterwards, as it continues to elongate, its convolutions become more and more numerous.

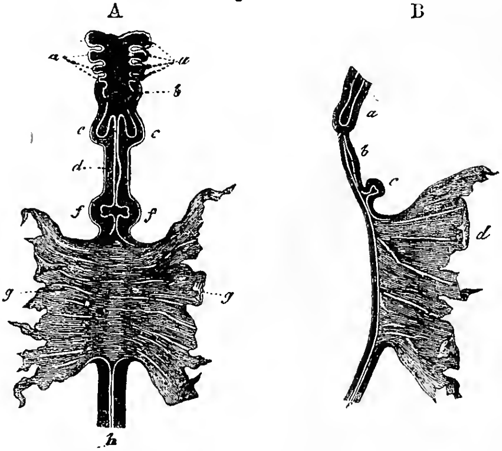
The *large* intestine is at first less in calibre than the small. In the

Fig. 788.—Early form of the alimentary canal (from Kölliker after Bischoff).

In A a front view, and in B an antero-posterior section are represented.

In A, *a*, four pharyngeal or visceral plates; *b*, the pharynx; *c*, *c*, the commencing lungs; *d*, the stomach; *f*, *f*, the diverticula connected with the formation of the liver; *g*, the yolk-sac into which the middle intestinal groove opens; *h*, the posterior part of the intestine. In B, *a*, the commencing lungs; *b*, the stomach; *c*, the liver; *d*, the yolk-sac.

Fig. 788.



early embryo there is at first no cæcum; but this part of the bowel gradually grows out from the rest, forming at first a tube of uniform calibre, without any appearance of the vermiform appendix: subsequently the terminal part of the diverticulum ceases to grow in the same proportion as the rest, and narrows into the appendix, whilst the proximal part attains its full development. The cæcum first appears as a protrusion a little below the apex of the bend in the primitive intestinal canal, and, together with the commencing colon, and the coils of small intestine, is lodged for a time in the wide part of the umbilical cord already mentioned as being next the body of the embryo. The ileo-cæcal valve appears at the commencement of the third month. When the coils of intestine and the cæcum have retired from the umbilicus into the abdomen, the colon is at first entirely to the left of the convolutions of the small intestines, but subsequently the first part of the large intestine, together with the mesocolon, crosses over the upper part of the small intestine, at the junction of the duodenum and jejunum. The cæcum and transverse colon are then found in the middle of the abdomen just below the liver; some time later the cæcum descends to the right iliac fossa, and the parts are nearly in the same position as in the adult.

At first, villous processes or folds of various lengths are formed throughout the whole canal. After a time these disappear in the stomach and large intestine, but remain persistent in the intermediate portions of the tube. According to Meckel, the villous processes are formed from

larger folds, which become serrated at the edge, and are thus divided into separate villi.

Hindgut.—The formation of the hinder part of the gut is complicated with the development of the allantois, which arises as a projection or out-growth of the mesoblast and hypoblast from the lower wall of its terminal portion, and which is therefore in connection internally with the hypoblastic lining of the cloaca.

Fig. 789.

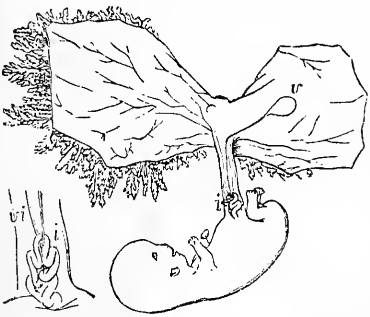


Fig. 789. — SKETCH OF THE HUMAN EMBRYO OF THE TENTH WEEK, SHOWING THE COIL OF INTESTINE IN THE UMBILICAL CORD. (A. T.)

The amnion and villous chorion have been opened and the embryo drawn aside from them; *v*, the umbilical vesicle or yolk-sac placed between the amnion and chorion, and connected with the coil of intestine, *i*, by a small or almost linear tube; the figure at the side represents the first part of the umbilical cord magnified; *i*, coil of intestine; *vi*, vitello-intestinal duct, alongside of which are seen omphalo-mesenteric blood-vessels.

Mesentery, Peritoneum and Diaphragm.—In the region of the pharynx and gullet the undivided mesoblast furnishes the outer coat of the alimentary canal, but in the stomach, and all the remainder of the gut, except at the anus, the separation of the two layers of mesoblast has taken place, and the visceral mesoblast furnishes the outer wall, together with the serous covering. In the thorax the right and left cavities remain distinct as the two pleuræ, while a portion still further forward is separated for the formation of the pericardium, and thus the gullet, as well as the lungs, is brought into relation with the pleuræ, and receives partial covering from them. The formation of the diaphragm, which does not at first exist, and which constitutes in mammals a partition between the thorax and abdomen, leads to the ultimate separation of the peritoneum from the pleuræ. Kölliker conjectures that the diaphragm may be formed by the advance of two halves from the dorsal and lateral regions, but the mode of origin of this partition is not yet sufficiently known (see Cadiat., No. 271), (His, No. 132, i. and ii.). Some examples of diaphragmatic hernia may be considered as arising from the persistence of the original connection between the two cavities. In the abdomen, also, the right and left peritoneal cavities are at first distinct, but when the intestine assumes a tubular form, these cavities are thrown into one across the middle plane of the body.

The peritoneum, like the rest of the lining of the body-cavity, is developed locally by superficial delamination from the mesoblast, and not from any special layer of formative tissue. The stomach is originally placed longitudinally in the abdomen, that part of it which afterwards forms the great curvature being situated dorsally and being attached by the simple mesogastrium. Very soon, a change of place occurs by which the pyloric part of the stomach and the duodenum pass to the right side, the left side of the primitive stomach thus coming to look ventrally and the right side dorsally. About the same time the mesogastrium is rapidly expanded and doubled upon itself so as to enclose a cavity,

while a fold of peritoneum connected with the liver, and arising from the ventral border of the stomach which has now become the lesser curvature, contracts round the entrance to the great omental cavity (behind the stomach and within the omentum) so as to form the gastrohepatic omentum and the foramen of Winslow (as first shown by Joh. Müller in 1830). The dorsal fold of the great omentum has not at first any connection with the transverse colon or its mesocolon, and there can be no doubt that it is only at a later period that it comes to be so closely united with them as to have given rise to the view, quite inconsistent with the history of its development now stated, that the transverse colon is enclosed between the two posterior layers of the omentum.

The occurrence of umbilical hernia in its various degrees may be referred to the persistence of one or other of the fœtal conditions in which a greater or less portion of the intestinal canal is contained in the

Fig. 790.

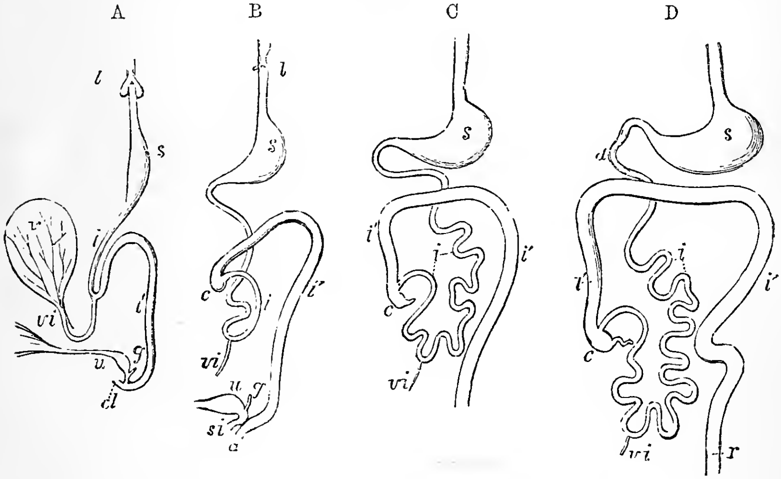


Fig. 790.—Outline of the form and position of the alimentary canal in successive stages of its development.

A, alimentary canal, &c., in an embryo of five weeks; B, at eight weeks; C, at ten weeks; D, at twelve weeks; *l*, the primitive lungs connected with the pharynx; *s*, the stomach; *d*, duodenum; *i*, the small intestine; *i'*, the large; *c*, the cæcum and vermiform appendage; *r*, the rectum; *cl*, in A, the cloaca; *a*, in B, the anus distinct from *si*, the sinus uro-genitalis; *v*, the yolk-sac: *vi*, the vitello-intestinal duct; *u*, the urinary bladder and urachus leading to the allantois; *g*, the genital ducts. In B, and C, the thickness of the colon is erroneously represented as greater than that of the ileum, and in C and D the cæcum as too far down and to the right.

umbilical cord; and it has been shown that the most common form of abnormal diverticula from the small intestine is connected with the original opening of the ductus vitello-intestinalis into the ileum.

Stomodæum.—The mouth, as elsewhere explained, is at first no part of the primitive alimentary canal, but is formed by involution of parts of the face, and receives, therefore, its lining membrane from epiblast. In this stage it has received the name of *stomodæum.* It is at first quite separated from the pharynx, which is the foremost part of the primitive alimentary canal, by the reflection of the layers of the blastoderm; and the com-

munication which is later established between the mouth and pharynx at the posterior arch of the fauces is due to a solution of continuity in these layers, which occurs in the chick at the end of the fourth day of incubation, and has been observed at a corresponding period of development in several mammals. The aperture has at first the form of a vertical slit, which widens later as it becomes the opening from the pharynx into the common cavity of the nose and mouth. The diverticulum of the pituitary gland occupies the place which becomes the top of the permanent pharynx, but is formed in connection with the epiblastic or buccal, and not the hypoblastic or pharyngeal division of the alimentary passage (see fig. 705, A and B, *f*).

Proctodæum.—To the anal invagination of the epiblast, in so far as it is separate from the primitive hypoblastic part of the hind gut, the name of *proctodæum* has been given.

In mammals there is very little anal invagination of the epiblast; in

Fig. 791.

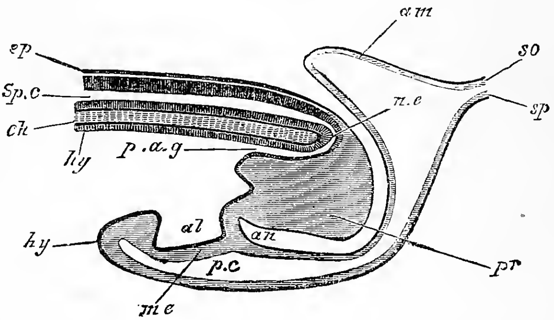


Fig. 791.—Diagrammatic longitudinal section of the hinder part of an embryo chick at the time of the formation of the allantois (from Balfour).

ep, epiblast; *Sp.c*, spinal canal; *ch*, notochord; *n.e*, neurenteric canal; *hy*, hypoblast; *p.a.g*, postanal gut; *pr*, remains of primitive streak folded in on the ventral side; *al*, allantois; *me*, mesoblast; *an*, place of future anus; *pc*, perivisceral cavity; *am*, amnion; *so*, body-wall; *sp*, visceral wall.

birds it is more extended from the development of the *bursa Fabricii* in connection with it, and the opening of the gut into the anus occurs at a comparatively late period, or not till the fifteenth day (Kölliker). In the rabbit the opening takes place on the eleventh or twelfth day. The subcaudal or postanal portion of the gut shrinks and disappears even before the opening takes place. The terminal portion of the gut remains behind the allantoid pedicle, and the whole of the tissues which close it thinning rapidly away, perforation takes place so as to form the primitive anal, or rather the cloacal opening. The separation of the permanent anus from the urogenital orifice, which occurs in all mammals excepting the monotremata, is the result of a later process of development, to be referred to in the next section. (Gasser, No. 272.)

THE LIVER AND PANCREAS.

The Liver.—The liver is one of the earliest formed abdominal organs. It consists at first, according to most observers, of a bifid mass of cells in connection with the lower surface of the duodenal portion

of the alimentary canal. A hollow cavity soon appears within the mass, which is the commencement of the main excretory duct (ductus choledochus communis). This cavity is lined by hypoblastic epithelium; and, according to the commonly received view, is produced as a diverticulum of the hypoblast of the intestine. Through the liver mass, but at first unconnected with its substance, there passes the main stem of the veins from the umbilical vesicle and allantois (umbilical vein or meatus venosus).

In the rudimentary mass composing the liver there are soon observed a number of solid cylinders of formative cells which branch out from the hypoblast into the mesoblast, and with this peculiarity belonging to the structure of the liver as compared with other glands, that, as these unite together by their ends and also laterally, they come at last to form a network of solid cords with which the hypoblastic diverticula are connected. In the meantime blood-vessels are developed in the mesoblast lying between the cylinders, which vessels become united as branches with the umbilical vein passing through the liver. Hollow processes also extend themselves from the hypoblastic diverticula and stretch into the solid cylinders of the hepatic parenchyma; but the greater part of this remains solid for a time, consisting of reticulated strings of cells between which there is nothing but blood-vessels.

According to Foster and Balfour, following Remak and the earlier observers, the cellular elements of the gland are stated to derive their origin from the hypoblast, and the mesoblast is mainly converted into blood-vessels and the fibrous tissue of the ducts.

The gall-bladder is formed by extension from the wall of the main duct.

The blood-vessels formed in the liver become branches of the main vein which passes through the cellular mass. These are distinguishable as an anterior and posterior set, the arrangement of which is such that the blood flows from stem to branches in the anterior, and from branches to stem in the posterior. Thus the distinction is established between portal and hepatic veins (see the Development of the Veins).

The solid cylinders of the blastema represent the hepatic lobular tissue, where the ducts are reticulated; the hollow processes the larger hepatic ducts, which do not communicate with one another. The origin of the finest ducts is not known; perhaps each cellular cylinder may be looked upon as a collection of hepatic cells, in the centre of which is the minute duct, according to the view now taken of the structure of the adult liver (Foster and Balfour).

The gall-bladder is at first tubular, and then assumes a pyriform shape. It first appears in the second month. The alveoli in its interior appear about the sixth month. At the seventh month it first contains bile. In the fœtus its direction is more horizontal than in the adult.

The following are the principal peculiarities in the liver of the human fœtus:—

Size.—At the sixth or seventh week, the liver is so large that it is said to constitute one-half of the weight of the whole body. This proportion gradually decreases as development advances, until at the full period the relative weight of the fœtal liver to that of the body is as 1 to 18.

In early fœtal life, the right and left lobes of the liver are of nearly equal size. Later, the right preponderates, but not to such an extent as after birth. Immediately before birth the relative weight of the left lobe to the right is nearly as 1 to 1·6.

Position.—In consequence of the nearly equal size of the two lobes, the posi-

tion of the fœtal liver in the abdomen is more symmetrical than in the adult. In the very young fœtus it extends over nearly the whole of the abdominal cavity; at the full period it still descends an inch and a half below the margin of the thorax, overlaps the spleen on the left side, and reaches nearly down to the crest of the ilium on the right.

Form, Colour, &c.—The fœtal liver is considerably thicker in proportion from above downwards than that of the adult. It is generally of a darker hue. Its consistence and specific gravity are both less than in the adult.

During fœtal life, the umbilical vein runs from the umbilicus along the free margin of the suspensory ligament towards the anterior border and under surface of the liver, beneath which it is lodged in the umbilical fissure, and proceeds as far as the transverse fissure. Here it divides into two branches; one of these, the *ductus venosus*, continues onward in the same direction, and joins the vena cava.

Fig. 792.

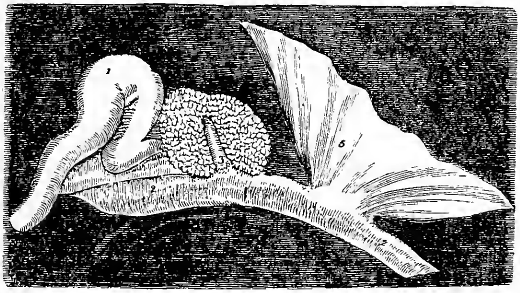


Fig. 792. — Early condition of the liver in the chick on the third day of incubation (from J. Müller). $\frac{10}{1}$.

1, the heart as a simple curved tube; 2, 2, the intestinal tube; 3, conical protrusion of the coat of the commencing intestine, on which the blastema of the liver (4) is formed; 5, portion of the layers of the germinal membrane, passing into the yolk-sac.

The other, which is the larger branch (the trunk of the umbilical vein), turns to the right along the transverse or portal fissure, and ends in the vena portæ, which, proceeding from the veins of the digestive organs, is in the fœtus comparatively of small dimensions. The umbilical vein, as it lies in the umbilical fissure, and before it joins the vena portæ, gives off large lateral branches, which pass directly into the right and left lobes of the liver. It also sends a few smaller branches to the square lobe and to the lobe of Spigelius.

After birth the umbilical vein becomes obliterated from the umbilicus up to the point of its giving off branches to the liver. The ductus venosus is also obliterated, but the veins which were given as branches from the umbilical vein to the liver remain in communication with and appear as branches of the left division of the portal vein.

The Pancreas.—This organ takes its origin in a mass of mesoblastic tissue, which thickens the wall of the duodenum close to the place where the rudiment of the liver is first seen, but placed more to the left side. This mass may be seen on the fourth day in the chick. There is, however, also a diverticulum from the primary wall of the intestine or hypoblast. Some doubt prevails, as in regard to the liver, with respect to the exact share of the hypoblastic and mesoblastic elements in the formation of the glandular cells. The main duct and its branches undoubtedly owe their origin to diverticula proceeding from the intestinal hypoblast, and the epithelial lining of the ducts is certainly derived from that source. By those who, adopting the most probable view, consider that the glandular cells also arise from the hypoblast, solid processes of that layer are described as stretching into the mass of mesoblast. Into these the diverticular cavities subsequently extend in more than one

main division. The blood-vessels and the connective tissue of the gland are undoubtedly due to the mesoblastic elements, and these are very soon combined with the parts proceeding from hypoblast.

Fig. 793.

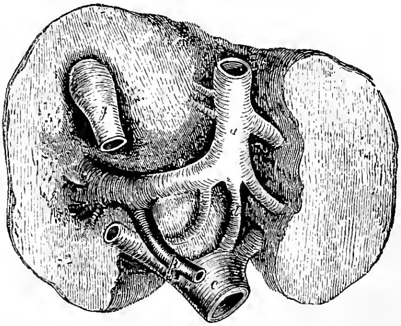


Fig. 793.—UNDER SURFACE OF THE FŒTAL LIVER, WITH ITS GREAT BLOOD-VESSELS, AT THE FULL PERIOD.

a, the umbilical vein, lying in the umbilical fissure, and turning to the right side, at the transverse fissure (*o*), to join the vena-portæ (*p*): the branch marked *d*, named the ductus venosus, continues straight on to join the vena cava inferior (*c*): some branches of the umbilical vein pass from *a* into the substance of the liver; *g*, the gall-bladder.

The development of the spleen is described along with that of the lymphatic system at p. 877.

THE LUNGS, TRACHEA, AND LARYNX, &c.

The very first appearance of the pulmonary organs in birds and mammals consists of a single median diverticulum from the ventral wall of the œsophagus immediately behind the fourth visceral cleft. The lower extremity of this protrusion soon becomes dilated towards the two sides, while its root communicating with the gullet remains single. These primitive protrusions or tubercles are visible in the chick on the third day of incubation, and in the embryoes of mammalia and of man at a corresponding stage of advancement. Their internal cavities communicate with the œsophagus, and are lined by a prolongation of the hypoblast.

The diverticulam of hypoblast is surrounded by a mass of mesoblastic

Fig. 794.

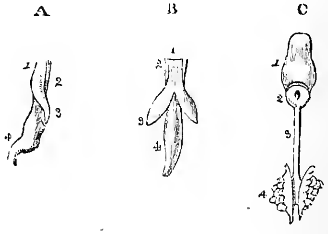


Fig. 794.—SKETCH ILLUSTRATING THE DEVELOPMENT OF THE RESPIRATORY ORGANS (from Rathke).

A, œsophagus of a chick, on the fourth day of incubation, with the rudimentary lung of the left side, seen laterally; 1, the front, and 2, the back of the œsophagus; 3, rudimentary lung protruding from that tube; 4, stomach. B, the same seen in front, so as to show both lungs. C, tongue and respiratory organs of embryo of the horse; 1, tongue; 2, larynx; 3, trachea; 4, lungs seen from behind.

cells, so that the pulmonary parenchyma, like that of the glands, owes its origin to both hypoblastic and mesoblastic elements. The substance of the mesoblast, thickening round the primary diverticula, becomes penetrated by secondary diverticula formed from the hypoblastic processes; these are succeeded by tertiary branches which develop the

bronchia, and ultimately have the air-cells formed as their terminations. The formative process consists essentially in the budding of hypoblastic into mesoblastic substance; the hypoblast furnishing the lining epithelium of the tubes, and the mesoblast the other tissues, such as muscular fibres, cartilage, blood-vessels, elastic tissue, &c.

Fig. 795.

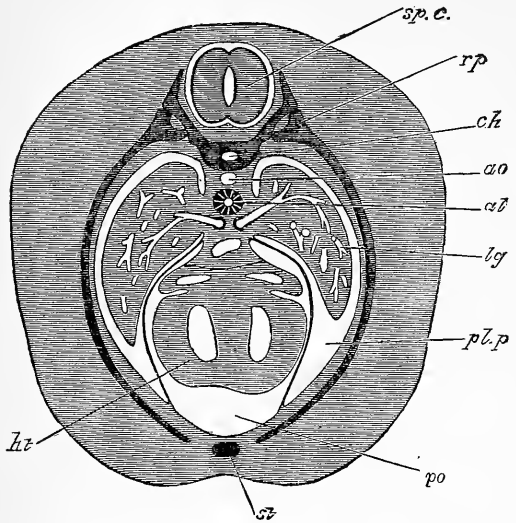


Fig. 795.—SECTION THROUGH AN ADVANCED EMBRYO OF A RABBIT TO SHOW THE RELATIONS OF THE PERICARDIAL AND PLEURAL CAVITIES (from Balfour).

ht, heart; *po*, pericardial cavity; *pl.p*, pleural cavity; *lg*, lung; *al*, alimentary tract; *ao*, dorsal aorta; *ch*, notochord; *rp*, rib; *st*, sternum; *sp.c*, spinal cord.

The division into larger lobes externally, three in the right and two in the left lung, may be seen at a very early period in the human fœtus. As the bronchial subdivision extends within the lungs, a tubercular or coarsely granular appearance is seen over the outer surface, as observed by Kölliker in the human fœtus in the latter half of the second month. This is produced by the primitive air-cells placed at the extremities of ramified tubes, which occupy the whole of the interior of the organ: the ramification of the bronchial twigs and multiplication of air-cells go on increasing, and this to such an extent that the air-cells in the fifth month are only half the size of those which are found in the fourth month.

In birds the principal air-sacs, three in number, are formed in direct connection with the lung in the course of its early development, and the rudiments of these sacs may be seen at an early period, as bulging constituent parts of the rudimentary lungs.

Pleuræ.—Each lung receives a covering externally from the lining membrane of the common pleuro-peritoneal cavity of its own side. This is at first only on the outer side; but, as the lungs enlarge, a fissure separates their solid substance from the outer wall of the œsophagus, and the pleura is carried round the lung-mass so as to encircle the gradually narrowing root of each lung. The two pleuræ remain separated by the mediastinum and heart, round which they have extended.

Pulmonary Vessels.—The blood-vessels of the lungs, which arise in the mesoblastic tissue, seem to be of comparatively late formation, penetrating into the pulmonary tissue only on the twelfth day in the chick. In mammals the blood-vessels are formed in the same manner in the pulmonary mesoblast. In birds, as before mentioned, the pulmonary arteries proceed one from each of the fifth arterial aortic arches, but in mam-

mals both right and left pulmonary arteries are connected with the fifth arch of the left side. The manner in which they become connected with the vessels formed in the lung-substance, and in which a union is established between the pulmonary veins and the left auricle, has not yet been ascertained.

Thyroid Body.—This seems to be the proper place at which a reference may be made to the two organs of doubtful nature—viz., the thyroid and thymus bodies—which have generally been ranked with the vascular glands, but which from their development appear to have also some close connection with the anterior part of the alimentary canal.

The thyroid gland takes its origin both in birds and mammals (W. Muller (No. 263), Kölliker (No. 28, i., p. 869), by a diverticulum from the ventral wall of the pharynx opposite to the place where the aortic bulb divides into the anterior visceral arches, and it is conjectured that it may be homologous with the endostyle or ventral diverticulum of the pharynx in the lampreys. It consists at first of a mass of hypoblast which in birds is hollow, but in mammals is solid; and in both classes large glandular cells are soon developed, which Kölliker represents in the rabbit as taking the form of reticulated cellular cords. The hypoblastic part soon acquires mesoblastic elements, in which blood-vessels and fibrous tissue are rapidly developed, and the thyroid body becomes highly vascular.

In birds the primary diverticular mass loses its connection with the pharynx at an early period, divides into two separate parts, and is carried back in the neck along with the elongation of that part, so as to form two very distinct compact spheroidal bodies situated near the division of the trachea.

In mammals the thyroid mass becomes somewhat bilobed, the larger lateral parts remaining united by the isthmus across the trachea.

In man the first origin of the thyroid body has not yet been observed. In the second and third months the glandular cords and follicular cavities begin to appear, and these go on increasing rapidly in the following months.

The Thymus Gland.—According to Kölliker's observations in the rabbit, this body is originally of epithelial nature, and arises as a diverticulum from an anterior pair of the visceral clefts, forming a small longish thick-walled triangular sacculus with two hollow tubular cornua. It soon divides into lobes, and in these gland-cells make their appearance, blood-vessels and other tissues being added from mesoblastic sources.

The view taken by Kölliker as to the origin of the thymus has been confirmed by the observations of Stieda in the pig and sheep, in which he found the thymus to arise as a paired outgrowth from the remnants of two visceral clefts; and he and Wölfler attribute a similar mode of origin to the thyroid body. (273 and 274.)

V. DEVELOPMENT OF THE URINARY AND GENERATIVE ORGANS.

I. GENERAL VIEW.

The development of the permanent urinary and generative organs has long been known to be intimately associated with that of the embryonic glandular organs named the primordial kidneys, or after their discoverer, C. F. Wolff, the Wolffian Bodies. This association was first ascertained

by H. Rathke, Oken, and Joh. Müller more than fifty years ago, and the fuller knowledge of its nature has been illustrated by numerous embryologists in investigations of more recent date (Bornhaupt, Kobelt, Kölliker, Waldeyer, Semper, Balfour and others).

Wolffian Bodies and Segmental Organs.—According to the two

Fig. 796.

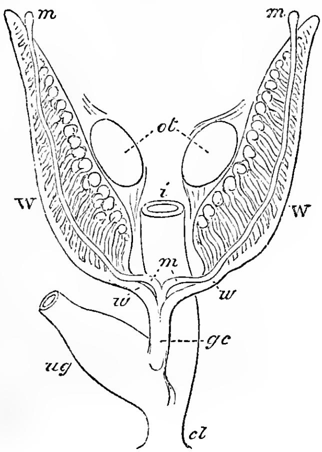


Fig. 796.—DIAGRAMMATIC OUTLINE OF THE WOLFFIAN BODIES IN THEIR RELATIONS TO THE RUDIMENTS OF THE REPRODUCTIVE ORGANS. (A. T.)

ot, seat of origin of the ovaries or testes; W, Wolffian bodies; *w. w*, Wolffian ducts; *mm*, Müllerian ducts; *gc*, genital cord; *ug*, sinus urogenitalis; *i*, intestine; *cl*, cloaca.

last named observers, the Wolffian bodies are the representatives in a certain stage of their development of a set of tubular glands or excretory organs existing in all vertebrates and in a certain number of invertebrate animals, especially annelida, to which the general name of *segmental organs* may be given, from their relations to the metameric somites of the body.

It was first shown by Rathke in 1826 that the Wolffian bodies of all vertebrates consist of glandular tubes with which are combined vascular glomeruli of the same general nature as those of the adult kidney; and recent researches have further shown that an essential structural character of the bodies in question, in the great majority of animals in which they are found, is the existence at an early stage of development of an opening on the one hand of a certain number of their tubes into the body cavity of the embryo, and on the other, of one or more of their main ducts into the cloaca or hinder part of the alimentary canal.

In the amniota, that is in reptiles, birds and mammals, while the greater part of the segmental organs known as the Wolffian bodies becomes atrophied and disappears in early fœtal life, a further development of organs of a similar structure gives rise to the permanent kidneys, and parts of the embryonic segmental organs with their ducts contribute to the formation of the adult male and female generative organs.

Distinction of Pronephros, Mesonephros, and Metanephros.—The simultaneous researches of Semper and Balfour in elasmobranch fishes have led them to distinguish three typical or fundamental parts of the segmental organs, all of which agree more or less, 1st, in their characteristic renal or combined tubular and glomerular structure, and 2nd, in their opening on the one hand anteriorly and internally into the abdominal cavity, and on the other posteriorly into the cloaca.

These bodies may be regarded as three serial divisions of an entire

segmental apparatus extending on each side of the body of a vertebrate embryo from the head or region of the heart to the cloaca in the hinder part of the body. The middle division, which in the embryonic condition is the largest, is the Wolffian body before referred to: the anterior, much smaller and less constant among animals, is the head-kidney of Balfour and Sedgwick; and the posterior one, later of being formed than the other two, corresponds to the permanent kidney of the amniota. To these several divisions of the segmental apparatus Ray Lankester has given the appropriate designations of Pronephros, Mesonephros and Metanephros.

Wolffian and Müllerian Ducts.—Each of these three divisions of the segmental organs possesses an excretory duct—viz., the Müllerian duct belonging to the pronephros or head-kidney, the Wolffian duct to the mesonephros or Wolffian body, and the ureter to the metanephros or permanent kidney of the amniota.

Fig. 797.

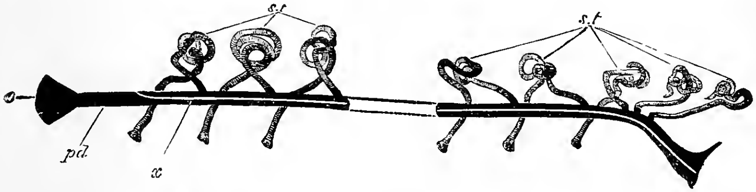


Fig. 797.—Diagram of the primitive condition of the kidney in an elasmobranch embryo (from Balfour).

pd, segmental duct; opening at *o*, into the body cavity and at its other extremity into the cloaca; *x*, line of separation between the Wolffian duct above and the Müllerian duct below; *st*, segmental tubes, opening at one end into the body cavity and at the other into the segmental duct.

The general nature and relations of these segmental organs, considered as embryonic structures, and as the foundation and precursors of the permanent urinary and internal generative organs, will be best explained by following Balfour's very clear statement of the principal steps of their development in elasmobranch fishes.

Origin and Formation of the Segmental Organs.—The segmental organs of the vertebrates originate in a long shaped mass of formative cells, which, at a period corresponding to the latter half of the second day of incubation in the chick, is seen to be separated from the mesoblast in a recess between its mesial or protovertebral and its lateral columns, and which has hence received the name of *intermediate cell-mass.* The separation of this cell-mass as a distinct cord or column begins in the region of the fifth somite or protovertebra in the chick, and extending from thence backwards to near the hinder part of the primitive gut, it finally reaches the cloaca with which it is connected. It is at first solid, but soon acquires a lumen within, and thus forms a tube, the greater part of which corresponds with that which was earlier known as the Wolffian duct, but which in its entirety, according to the more recent views before quoted, may be named the *segmental duct.* This column with its duct at the same time changes its position by sinking down in a ventral direction, so that it comes to project in the body-cavity, and soon, by a rapid increase of formative substance round

it, the whole forms a longitudinal column on each side of the mesentery between the parietal and visceral divisions of the mesoblast.

Segmental Tubes.—Within this columnar mass a series of tubular offsets are early developed (Wolffian tubes) which have the general form of short

Fig. 798.

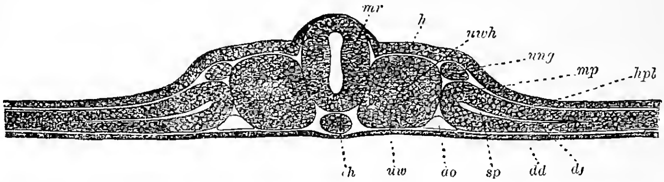


Fig. 798.—Transverse section through the embryo of the chick and blastoderm on the second day (from Kölliker).

d d, hypoblast; *ch*, chorda dorsalis; *u w*, primordial vertebræ; *m r*, medullary plates; *h*, corneous layer or epiblast; *u w h*, cavity of the primordial vertebral mass; *m p*, mesoblast dividing at *s p* into *h p l*, body wall, and *d f*, visceral wall; *u n g*, Wolffian duct, beginning in the intermediate cell-mass. (See also figs. 690 and 692.)

transverse cæca directed inwards and connected externally with the main segmental duct. These tubes in the lower vertebrates, and in reptiles among the amniota, correspond closely in number with the vertebral or muscular somites in the region which they occupy; but in birds and mammals, though at first nearly so corresponding, they come later to

Fig. 799.

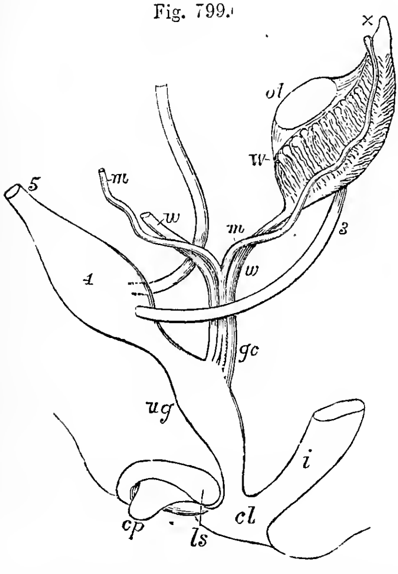


Fig. 799. — Diagram of the primitive uro-genital organs in the embryo previous to sexual distinction.

The hinder parts are shown chiefly in profile, but the Müllerian and Wolffian ducts are seen from the front, entire upon the left and cut short upon the right side. 3, ureter; 4, urinary bladder; 5, urachus; *ot*, the genital ridge from which ovary or testicle is afterwards formed; W, left Wolffian body; ×, anterior part from which the coni vasculosi are afterwards developed; *w.w*, right and left Wolffian ducts; *m.m*, right and left Müllerian ducts uniting together and with the Wolffian ducts in *gc*, the genital cord; *ug*, sinus urogenitalis; *i*, lower part of the intestine; *cl*, cloaca; *cp*, elevation which becomes clitoris or penis; *ls*, fold of integument from which the labia majora or scrotum are formed.

be more numerous by the addition both of original and of secondary tubes. These may be named the *segmental tubes*. In its primary form, therefore, the segmental organ might be described as consisting of a main duct or canal with a number of cæcal tubuli branching from it or leading into it laterally.

Very soon, however, a great modification and complication in the structure and relations of this organ takes place in three ways which may be shortly stated as follows :—1st, by the formation of openings from the inner ends of some of the segmental tubes, and later of the segmental duct itself into the peritoneal or body cavity at its upper or dorsal part; 2nd, by the increased growth and convolution of the tubules, especially of the mesonephros, and by the development of vascular glomeruli in connection with them; and 3rd, by the formation of a new collateral duct in the vicinity of the original segmental duct, and certain changes in the association of the segmental tubes with the two ducts which thus come to take the place of the original segmental duct. These latter changes are of such a nature that the greater number of the

Fig. 800.

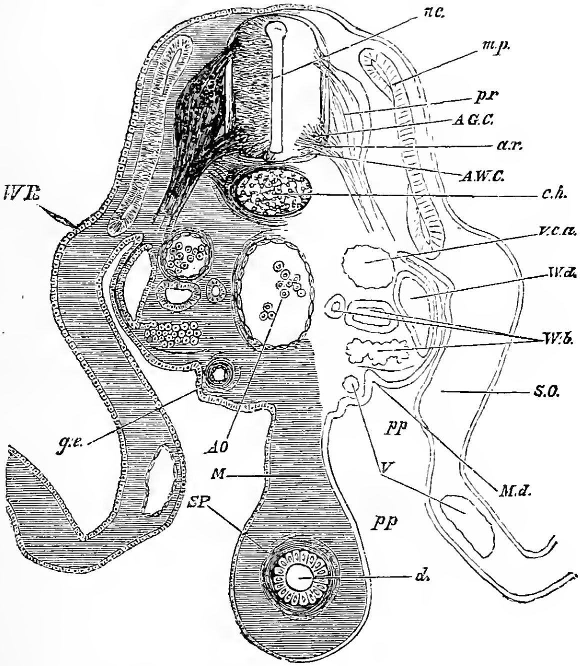


Fig. 800.—Section through the lumbar region of an embryo chick of four days (from Foster and Balfour).

nc, neural canal; *pr*, posterior root and ganglion of a spinal nerve; *ar*, anterior root; *mp*, muscle-plate; *ch*, notochord; *WR*, Wolffian ridge; *AO*, aorta; *Vc a*, cardinal vein; *Wd*, Wolffian duct; *Wb*, Wolffian body with glomeruli; *ge*, germinal epithelium; *Md*, depression forming the commencement of the Müllerian duct; *d*, alimentary canal; *M*, mesentery; *SO*, body-wall; *SP*, visceral wall; *V*, blood-vessels; *pp*, pleuro-peritoneal space.

glandular tubules forming the mesonephros remain connected with that part of the segmental duct which becomes the Wolffian duct, and are thus brought to a common opening in the cloaca; while (as ascertained in some vertebrates, though not in all) some of the anterior tubules are left in connection with the separate or newly-formed duct,

which, having been originally discovered by Joh. Müller in 1830, has since been named the Müllerian duct.

The ureter may be looked upon as an offset from the hinder part of the Wolffian duct, and the metanephros of the elasmobranchs consists of a set of segmental tubes developed in connection with this duct, possessing the same glandular and glomerular structure as the mesonephros, and occupying a situation which is on the dorsal aspect of the Wolffian duct and near its hinder part. The characteristic feature in the development of the urino-genital system in the amniota is according to Balfour the formation of a metanephros or permanent kidney, and the complete or partial disappearance of the other two parts of the segmental organs—viz., the pronephros and mesonephros.

The Müllerian and Wolffian ducts stand in a different relation to the productive organ in the two sexes. In the female the Müllerian duct becomes developed into the whole length of the genital passages, and the Wolffian duct almost entirely disappears. In the male, on the other hand, the Wolffian duct becomes converted into the excretory duct (vas deferens) of the testicle; while the Müllerian duct undergoes atrophy and has no permanent existence.

Fig. 801.

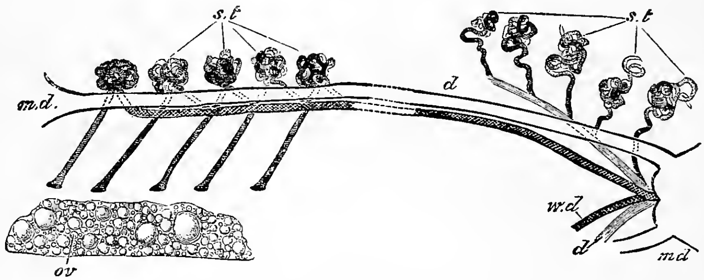


Fig. 801.—Diagram of the arrangement of the urino-genital organs in an adult female elasmobranch (from Balfour).

m.d., Müllerian duct; *w.d*, Wolffian duct; *s.t*, segmental tubes; five of them are represented with openings into the body cavity, and five posteriorly correspond to the metanephros; *ov*, the ovary; *d*, ureter.

In connection with the conducting passages of both sexes there are found in later life vestiges of those of the embryonic structures which are not employed in the production of the permanent generative organs, and these vestiges are of considerable interest in their bearing upon the history of the changes by which the permanent organs are formed.

Genital Ridge and Germ-Epithelium.—In all the Vertebrates the productive gland of the generative system, ovary or testicle, takes its origin from formative blastema situated on the mesial side of each Wolffian body or mesonephros at an early period of embryonic life, and there is in the commencement a close connection between the origin of the first elements of the sexual products, ova or spermatic cells, and a portion of the epithelium which lines the body cavity in that region. Here an elevation of the blastema and thickened epithelium marks the presence of the *genital ridge*, and the name of *germ-epithelium*

is given to the more developed portion of the epithelium from which the generative elements are derived.

In the lower vertebrates the anterior part of the Müllerian duct is connected with the pronephros, and the opening by which this duct communicates at its anterior extremity is probably one of the peritoneal apertures of that portion of the segmental organs. Among the amniota the pronephros or head-kidney is as yet only known in birds by the researches of Sedgwick and Balfour; but, according to the views of the latter, it seems probable that the anterior part of Müller's duct is, in reptiles and mammals as well as in birds, homologous with the duct of the pronephros. Although, therefore, the tubular part of the pronephros is not developed in these animals, there is reason to hold that the type of development of their urogenital passages is, in the main, the same as in birds and the lower vertebrates.

The relation of the origin of the productive sexual organs to the mesonephros, though not yet fully ascertained, is known to be closer in the male than in the female sex. Thus there is good reason to believe that, while in both sexes, as already stated, the productive elements are derived from the germinal cells of the genital ridge, there are

Fig. 802.

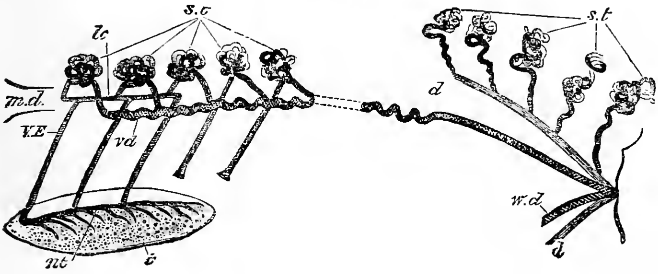


Fig. 802.—Diagram of the arrangement of the urino-genital organs in an adult male elasmobranch (from Balfour).

m.d., rudiment of Müllerian duct; *w.d*, Wolffian duct, serving at *vd* as vas deferens; *s.t*, segmental tubes, two represented with openings into the body cavity; *d*, ureter; *t*, testis; *nt*, canal at the base of the testis; V.E, vasa efferentia; *lc*, longitudinal canal of the Wolffian body.

differences in the further development of the organs containing the generative elements, as in the Graafian follicles in the one and the spermatic tubes in the other.

The External Organs.—With regard to these organs, it is sufficient to remark in this place that the structural elements from which they take their origin are essentially the same in the two sexes, and that their special sexual characters in the male and female depend rather upon differences in the degree and manner of their development than upon any fundamental disparity in their nature. The nature of the process will be more fully explained hereafter.

In all mammals, with the exception of the monotremata, the distinctive development of the external organs is preceded by the separation of the cloaca internally into an anterior urogenital and posterior anal part, which when the proctodæum is perforated open separately on the surface.

The history of the development of the parts composing the external organs in connection with the formation of their special sexual characters will be described in a later part of this chapter.

II. FURTHER DEVELOPMENT OF THE PERMANENT URINO-GENITAL ORGANS.

I. THE KIDNEYS.

The origin of the kidneys as a metanephros in connection with the hinder part of the Wolffian body on its dorsal aspect has already been adverted to. Kölliker, following Kupffer and Lieberkühn, and from his own observations, has described the first appearance of the kidney in mammals as taking place by the development of a tubular diverticulum from the Wolffian duct near its termination in the cloaca. This tube represents the earliest condition of the ureter, and it extends into a mass of mesoblastic cells corresponding or continuous with that of the Wolffian body from which the glandular part of the kidney is gradually developed. The distinction between the tubular or ureter part and that which is to become the parenchyma of the gland becoming more apparent, the latter increases greatly in volume, and rapidly encroaching on the space above the Wolffian body comes to occupy the whole of the region between it and the aorta, and even to project further forward, while other changes in the interior indicate the process of formation of the gland. In the ureter the hinder part elongates as a single tube, but the forepart becomes dilated and subdivided into cæca or wider portions which represent the commencement of the several divisions of the pelvis. These divisions are surrounded by masses of the glandular blastema, into which there pass smaller cæcal tubes which seem to sprout from the pelvic hollows of the original ureter. These tubes then become convoluted, and on their exterior small masses of cells accumulate in which the vascular glomeruli are gradually formed by the development of blood-vessels within them. These blood-vessels remain connected with the external blastema in which they arise by means of a stalk or pedicle, but the glomerulus now comes to be projected into a doubling of the uriniferous tubule in the manner which belongs to all such renal structures. There is at first no distinction between the straight and the convoluted parts of the tubular substance, but this arises later by the gathering together of the convoluted parts in rounded masses towards the exterior, and the elongation of the straighter tubes internally, while at the same time or somewhat later the latter group themselves into bundles which form the pyramids and project into the pelvic calices.

In the human fœtus of eight weeks, the Malpighian glomeruli are already apparent. In the third month the papillæ are formed, and in the fourth the recurved tubes of Henle have become apparent. At first, therefore, the kidneys seem to consist wholly of cortical substance, with only convoluted tubes, and the formation of the straight tubular substance is the result of a later change. The tubes are absolutely, as well as relatively, wider in early fœtal life than in the adult.

In the human fœtus of ten weeks the kidneys have acquired their peculiar bean-like shape with the hilus for the ureter, pelvis and vessels. They are also distinctly lobulated externally, and they retain this form up to the time of birth, and during the first year of infancy, and it is not uncommon to find the lobulated form in kidneys of a later period.

Urinary Bladder and Urachus.—The urinary bladder, as already stated in an earlier part of this description, is formed by a dilatation of the stalk of the allantois. In the human fœtus this appears as a spindle-shaped cavity at the end of the second month, the narrower part below being prolonged as the first part of the urethra into the cloaca, while the upper narrowing part extends as the urachus into the umbilical cord, and at an early period in animals is prolonged into the cavity of the allantois.

The ureters terminate in the dorsal wall of that part of the urogenital sinus which is dilated into the urinary bladder.

The urachus is usually a solid cord at a short distance from the bladder, but, according to Luschka, it not unfrequently remains hollow for some length within the umbilical cord.

The spindle shape of the bladder is retained for a long time in the human fœtus.

For the development of the Suprarenal bodies, see p. 841.

Genital Cord.—In both sexes, as was first fully shown by Tiersch (No. 287) and Leuckart (No. 287*) in 1852, the two Wolffian ducts are united by surrounding substance into one cord behind what becomes the base of the urinary bladder; but retaining internally their separate passages until they reach the sinus urogenitalis. With this cord the Müllerian ducts are incorporated posteriorly, so that at one time there are four passages through the whole of the genital cord. The Müllerian ducts next coalesce into one at some little distance from their lower ends, and this fusion progressing upwards and downwards for a considerable space, a single median cavity is produced which lies between the still separate canals of the Wolffian ducts. A large accumulation of tissue in its walls gives to the genital cord great thickness as compared

Fig. 803.

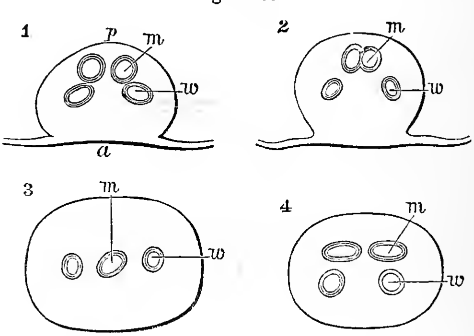


Fig. 803.—Transverse sections of the genital cord in a female calf embryo. Magnified 14 diameters (from Kölliker).

1, near the upper end; 2 and 3, near the middle; 4, at the lower end; *a*, anterior, *p*, posterior aspect; *m*, Müllerian ducts united or separate; *w*, Wolffian ducts.

with the neighbouring parts of the ducts where they emerge from its enclosure. The lower part of the united Müllerian ducts thus comes afterwards to form the foundation of the vagina and lower part of the uterus in the female, and the corresponding prostatic vesicle with its occasional vestigial accompaniments in the male, or the uterus masculinus.

II. GENERATIVE ORGANS.

In the history of the further development of the generative organs it will be convenient to consider them in the two sexes in succession under the three heads of, 1st, the reproductive glands, or strictly internal

organs; 2nd, the conducting passages or intermediate organs; and 3rd, the external organs.

1. **Reproductive Glands.**—From all recent researches it appears certain, as previously stated, that the reproductive elements of the two sexes take their origin from an identical source, viz., the germ-epithelium of the genital ridge, situated on the mesial side of each Wolffian body. It appears further that in the earliest stages of both the sexes the thickening of the genital ridge by the columnar enlargement of its epithelial cells occurs nearly in like manner; and it is even further stated that, in embryoes exhibiting a tendency to be developed as males, an enlargement of some of the germ-epithelial cells into the form of primordial ova is observed of the same kind as in embryoes about to become females. But as development advances, the similarity in the condition of the genital ridge becomes less, and the germ-epithelial cells remain on the whole flatter in the male than in the female.

In the human embryo the distinction of sex begins to be perceptible in the internal organs in the seventh week, and becomes more apparent in the eighth. The reproductive gland is from the first connected with the Wolffian body, with which its blastema seems to be actually in part continuous; and it remains attached to it, or after its disappearance, to the structure which occupies its place, by a fold of the peri-

Fig. 804.

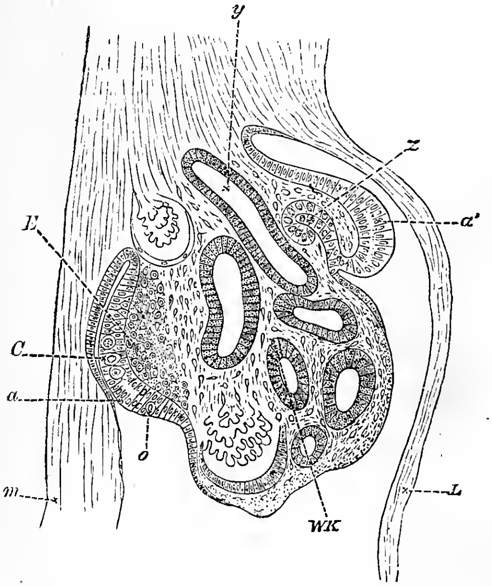


Fig. 804.—Transverse section of the Wolffian body of the chick developing the pronephros and genital gland on the fourth day (from Balfour after Waldeyer).

m, mesentery; *L*, body-wall; *a'*, portion of the epithelium from which the involution of the anterior part of the Müllerian duct *z*, is taking place; *a*, thickened germinal epithelium in which are seen primitive germinal cells, *C* and *o*; *E*, modified mesoblast which will form the stroma of the ovary; *WK*, Wolffian body; *y*, Wolffian duct.

toneal membrane, constituting the mesorchium or mesovarium. Upper and lower bands fix the Wolffian body; the upper passing to the diaphragm may be named the diaphragmatic; the lower, running down towards the groin from the Wolffian duct, contains muscular fibres and constitutes the future gubernaculum testis and round ligament of the uterus.

In birds the distinction of sex is easily recognisable at an early period by the occurrence in the female of an atrophy of the ovary and passages on the right side, while those of the left are fully developed.

The Testicle.—In male human embryoes at the tenth week already seminal canals are visible, being at first, according to Kölliker, entirely composed of cells, but by the eleventh and twelfth weeks the tubes have become somewhat smaller, longer, and are now branched and possess a membrana propria. There is also by the end of the third month a commencement of lobular division, and the body of the testis is now covered with a condensed layer of fibrous tissue which forms the tunica albuginea. The serous covering is derived from the abdominal peritoneum.

The first origin of the glandular substance of the testis has not been observed in the human embryo, but from the observations of Egli in male embryo rabbits (No. 308) it appears that the epithelial cells, which remain smaller than in the females, soon become connected with the deeper blastema extending towards the Wolffian body, and form strings of cells running into the body of the future testis. These are the commencements of the tubuli seminiferi. Some intimate connection, however, also exists between the tubular structure of the testis and the tubes of the anterior part of the Wolffian body.

Fig. 805.

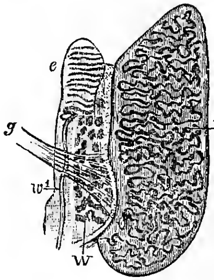


Fig. 805.—Internal genital organs of a male human embryo of $3\frac{1}{2}$ inches long (from Waldeyer).

t, body of the testicle with seminal canals formed ; *e*, epididymis, or upper part of Wolffian body ; *w*, Wolffian body, lower part, becoming paradidymis or organ of Giraldès ; *w'*, Wolffian duct, becoming vas deferens ; *g*, gubernaculum.

The nature of this connection is not fully made out in birds or mammals, but, from the observations of Braun in reptiles (No. 303*), it is probable that the formation of the seminiferous tubes has some close relation with the segmental tubes of the Wolffian body, and in such a way that the germinal epithelium cells are combined with, or enclosed in these tubes, which extend into the body of the testis, and thus come to contain the rudiments of the spermatic cells. (For the development of the spermatozoa from the spermatic cells, see p. 698 of this volume.)

To the probable union between the tubular structure of the testis (rete testis, vasa recta, &c.) with the vas deferens, through the coni vasculosi, by the persistence of some of the tubes in the anterior part of the Wolffian body, reference will be made under the description of the development of the genital passages.

The general result of recent researches appears to be that the elements of the spermatozoa, as formed in the spermatic cells, are derived from the germinal epithelium, while the secreting tubes, which contain the cells, owe their origin to a development of formative mesoblast situated between the germ-epithelium and the Wolffian body, and probably also to the direct extension of some of the segmental tubes from the Wolffian bodies.

The Ovary.—Considered as a glandular organ the ovary differs from the testicle and other glands by the absence of special excretory ducts, and by the separation of its conducting passages from the glandular or productive part of its structure. Like the testicle it begins to manifest its peculiar characteristics by the seventh or eighth week, when the germ-epithelium has attained considerable thickness, and forms a decided

prominence on the mesial side of the Wolffian body. The farther development of the glandular part of the organ consists mainly in the formation of ovigerms and ova, and the enclosure of these in Graafian follicles by a peculiar combination or intermixture of the germinal cells from the surface with the deeper blastema which forms the stroma of the organ.

Fig. 806.

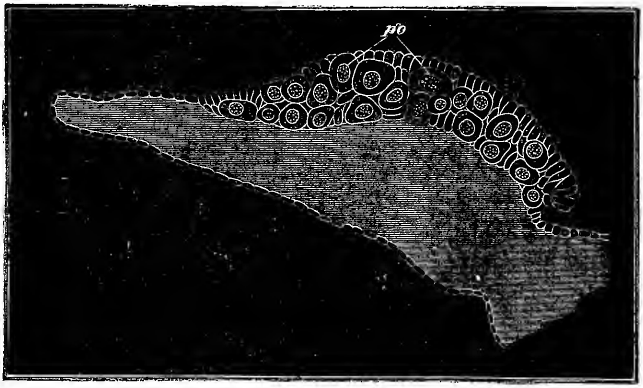


Fig. 806.—Transverse section through the ovary of an embryo shark, showing the germ-epithelium passing into primitive ova (from Balfour).

At *po*, the prismatic germ-epithelium and two primitive ova of which one is still on the surface, the other has sunk below the epithelium; elsewhere the lightly-shaded part of the figure shows the ovarian stroma or lymphatic tissue and the covering of ordinary epithelium.

Primordial Ova.—From the researches of Waldeyer (No. 58) and of many others there cannot now be any doubt that the primitive ova

Fig. 807.

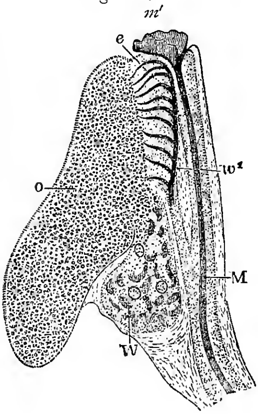


Fig. 807.—Internal organs of a female human fœtus of $3\frac{1}{2}$ inches long, or about 14 weeks. Magnified (from Waldeyer).

o, the ovary full of primordial ova; *e*, tubes of the upper part of the Wolffian body forming the epoophoron (parovarium of Kobelt); W, the lower part of the Wolffian body forming the paroophoron of His and Waldeyer; *w′*, the Wolffian duct; M, the Müllerian duct; *m′*, its upper fimbriated opening.

are derived from some of the cells of the germ-epithelium which undergo enlargement and subsequently become enclosed in Graafian follicles. But doubts have existed as to the exact manner in which this enclosure takes place, and more especially as to the source of the cellular lining of the follicle which is allied to epithelium and gives rise to the so-called granular membrane of later periods. According to the view first advocated by Waldeyer, the cells

which form this epithelial and granular-cell lining of the follicle proceed originally from the germ-epithelium along with the primitive ova. By Foulis, on the other hand, the origin of these cells has been attributed to an enclosure and differentiation of the cells of the ovarian stroma, while Kölliker's observations have led him to adopt the view that they proceed from the cellular contents of tubes which are connected with the Wolffian body, and remain for a time as vestiges in the base of the ovary (paroophoron?). But the observations of Ludwig (No. 59) and Balfour (No. 62) seem to show very decidedly that in the lower vertebrates the epithelial lining of the primitive follicle is the direct product of cells which, like the ova themselves, proceed from the germ-epithelium. And though it must be admitted that in the human embryo there are appearances favourable to the view taken by Foulis, the writer of this is induced from his own observations in the human ovary and that of several mammals now to give a preference to the opinion of Waldeyer.

Fig. 808.

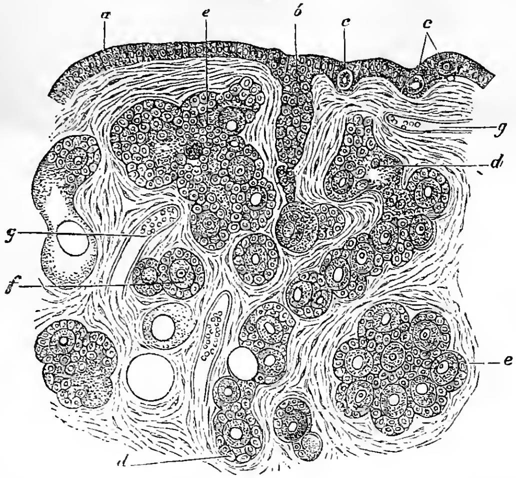


Fig. 808.—Section of the ovary of a newly-born child. Highly magnified (Waldeyer).

a, Ovarian or germinal epithelium; *b*, formation of an ovarian tube; *c*, *c*, primordial ova lying in the germ-epithelium; *d*, *d*, longer tube becoming constricted so as to form nests of cells; *e*, *e*, larger nests; *f*, distinctly formed follicle with ovum and epithelium; *g*, *g*, blood-vessels.

In the earliest stages of ovarian development, and for a considerable time afterwards, the germinal cells of the genital ridge undergo a remarkable multiplication, and many of them while still close to the surface, become much larger than the rest, and assume the appearance of primordial ova; the nucleus expanding into the germinal vesicle, with a distinct nucleolus (or macula) formed within it, and the external protoplasm increasing greatly to form the vitellus or yolk, but, at first, without any enclosing membrane.

As these ovigerms increase in number and size they retire from the surface of the germinal ridge or ovary, and, collecting into groups, they sink into the blastema which lies below the epithelial covering.

At the same time a great increase and extension outwards of the deeper

blastema occurs, and the lymphatic cells (Balfour) of which it consists, present more and more the appearance of connective or fibro-nuclear tissue.

Ovarian Tubes and Nests.—Ere long the groups of ovigerms become enclosed in prolongations of the stroma, which in some animals present a marked tubular form, as described first by Valentin (No. 281), and afterwards more fully by Pflüger (No. 55), and in other instances assume the spherical or grape-like form, so as to deserve rather the name of *nests* which has been applied to them.

Fig. 809.

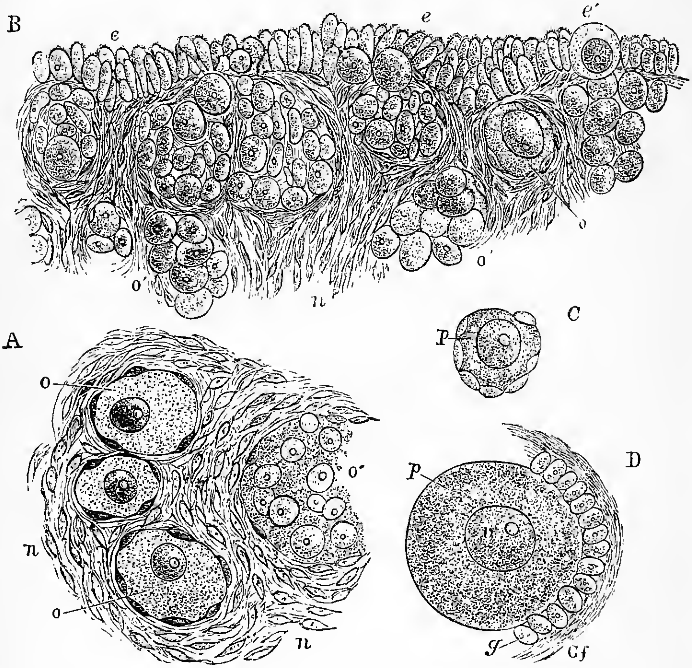


Fig. 809.—Views of the formation of ova and Graafian follicles in the ovary (from Foulis).

A, small portion of the ovary of a human fœtus of $3\frac{1}{2}$ months, showing primordial ova embedded in the stroma ; *o*, larger primordial ova ; *o'*, cluster of earlier ova ; *n*, fusiform corpuscles of the stroma. B, portion of the ovary near the surface in a human fœtus of $7\frac{1}{2}$ months, showing the manner of inclusion of the germ-epithelium corpuscles in groups in the ovarian stroma ; *e*, germ epithelium ; *e'*, one of the cells enlarging into a primordial ovum before sinking into the stroma ; *o*, a larger cell imbedded, becoming an ovum ; *o'*, groups of ovigerms or germ cells which have been surrounded by the stroma. C, young ovum from the same ovary, isolated ; *p*, yolk protoplasm. D, ovum more advanced, enclosed in condensed stroma, which begins to form a Graafian follicle ; *p*, yolk protoplasm ; *v*, germinal vesicle with macula ; *g*, the enclosed corpuscles now converted into the granular cells ; *Gf*, condensed stroma forming the wall of the Graafian follicle.

In these tubes and nests the enlarged cells derived from the epithelium, or ovigerms, are at first of nearly uniform size and appearance, but very soon some of them undergo a greater enlargement, while the others diminish in size, and lose the spherical form. It is not improbable that many of these last may wholly disappear, having served, according to Balfour's view (No. 62), as pabulum, or food, to those which continue to grow. The result of the whole is, however, that one, or it may be more, of the cells undergo increased development, and acquire

more and more distinctly the characters of ova by the enlargement of the yolk protoplasm and germinal vesicle, while those of the others which survive alter their shape, becoming flattened nucleated cells, and arrange themselves as a more or less complete single layer of epithelium lining the cavity of ovarian stroma in which the primordial ovum is now situated. This cavity is of course the first stage of the Graafian follicle, and the single layer of epithelium lining it, or covering the ovum, is the commencement of the cellular lining which afterwards becomes largely developed in the tunica granulosa.

Enclosure in Graafian Follicles.—While this is going on, and at a time which varies considerably in different animals, but is comparatively early in the human ovary, the ovarian stroma has advanced rapidly so as to enclose first the groups of primordial ova in the tubes and nests, and then the individual ova, with their still very imperfect epithelium; and the wall of the Graafian follicle comes to be formed by a layer of condensed stroma surrounding each space containing an ovum. In many animals the ova remain in this condition for a long time, occupying the germinal stratum at a short distance from the surface of the ovary, as may be most distinctly seen in the ovary of the kitten (see figs. 612 and 613, p. 715), and this stratum of primordial ova is even recognisable in some animals of adult age. In the human ovary the tubes and nests are more equally diffused through the substance of the ovary than in most animals, and, indeed, so much so, and in such numbers, that in the human embryo of from four months up to the period of birth the ovary seems to be an entire mass of primordial ova, with only a slight admixture of the stroma and other tissues; and it is calculated that in the earlier part of this stage the ovaries of the human fœtus may contain not fewer than 70,000 cells having all the characters of primordial ova.

Wall of the Follicle.—When, however, a certain number of the ova begin to be further developed, they retire from the surface into the deeper stroma of the ovary, the most advanced being generally situated at the greatest depth, but at some distance from the hilus. (See fig. 615, p. 719.) When this takes place, we observe, along with the enlargement of the parts both of the ovum and follicle, other changes. The ovarian stroma, or fibro-nuclear tissue, forms layers round the follicle, being firmer and more fibrous externally, and looser with somewhat rounder cells next the cavity, and into the inner of these layers a rich network of blood-vessels soon penetrates. In the more advanced stage, also, we can distinguish a fine homogeneous limiting or basement membrane within.

Granular-cell Lining.—In the interior, and surrounding the ovum, the epithelial cells, which were at first flat and sparse, have now been multiplied, and have assumed the prismatic shape, so as to give a complete and compact lining to the follicle. In subsequent stages the cells of this epithelial lining rapidly increase, so as to form at first several, and then more numerous layers; and when the follicle has attained some size a fissure occurs in these granular cell layers on one side, which leaves the ovum surrounded by a set of the cells which are in contact with the wall of the follicle, while the interval gradually increasing between the ovum so enclosed and the opposite wall of the follicle, there is thus produced the follicular cavity. In the much greater expansion of the follicle which accompanies full maturation of the ovum, it is mainly by the accumulation of fluid in this cavity that the enlargement is produced.

In the ovum itself changes also take place, first of all by some increase of size, which however remains greatly inferior to that of the follicle, so that while the follicle may attain the diameter of from $\frac{1}{10}$ to $\frac{1}{5}$ of an inch, the ovum rarely goes beyond $\frac{1}{200}$ or $\frac{1}{150}$. The reticular structure of the protoplasm in the germinal vesicle becomes more distinct, the macula well defined, the yolk-protoplasm proportionally increased in size and exhibiting yolk corpuscles, and a zona pellucida, or external membrane, gradually makes its appearance externally, being probably due to a condensation of the outer part of the yolk-protoplasm.

The primordial ovum, when first formed, has a diameter of about $\frac{1}{1200}$ to $\frac{1}{1500}''$, and its germinal vesicle, or nucleus, which is then proportionally large, may be about $\frac{1}{2500}$ of an inch in diameter. When the granular epithelium has become cylindrical, and the single ovum enclosed in a simple Graafian follicle begins to sink more deeply into the ovarian substance, its diameter is nearly doubled, while

the Graafian follicle is not larger than sufficient to contain it and its epithelial covering. As the ova approach maturity the Graafian follicle expands rapidly, both by an increase of its fluid and of the granular cells, while the ovum remains of comparatively small size.

2. **The Genital Passages.**—The existence at first of two sets of tubes between the internal productive organs and the external parts has already been adverted to as a feature common to both sexes. The female organs contrast with those of the male in the passages of the first being formed by the large development of one of these sets of tubes, viz., the Müllerian ducts, and in the abortive disappearance of the greater part of the other or Wolffian ducts; while in the male the ducts of Müller suffer in a great measure the abortive retrogression, and the seminal conducting tubes are produced from canals formed out of special parts of the Wolffian body and the whole of the Wolffian duct. But as in all embryoes of whatever sex both sets of tubes are originally present, while a different one of the primary tubes becomes developed into the respective permanent conducting passages, vestiges of the other primary tubes, as already stated, are always present in various degrees in both sexes.

The Female Passages.—In the female, the vagina, uterus, and

Fig. 810.

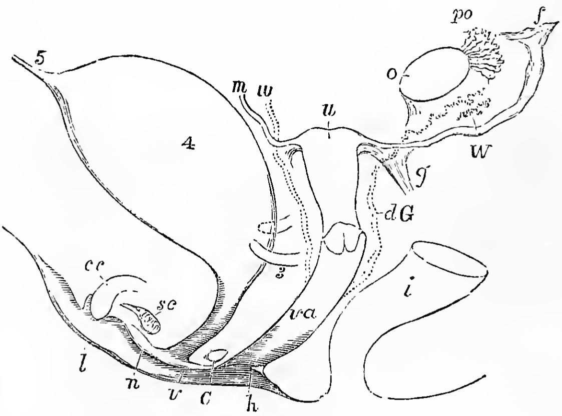


Fig. 810.—Diagram of the female type of sexual organs.

This and figure 813 represent diagrammatically a state of the parts not actually visible at one time; but they are intended to illustrate the general type in the two sexes, and more particularly the relation of the two conducting tubes to the development of one as the natural passage in either sex, and to the usual occurrence of vestiges of the other tube, as well as to the persistence of the whole or parts of both tubes in occasional instances of hermaphroditic nature.

3, the ureter joining the urinary bladder; 4, urinary bladder; 5, urachus; *o*, the left ovary nearly in the place of its original formation; *po*, parovarium, epoophoron of Waldeyer; W, scattered remains of Wolffian tubes near it, paroophoron of Waldeyer; *d* G, remains of the left Wolffian duct, such as give rise to the duct of Gaertner, represented by dotted lines; that of the right side cut short is marked *w*; *f*, the abdominal opening of the left Fallopian tube; *u*, the upper part of the body of the uterus, still presenting a slight appearance of division into cornua; the Fallopian tube of the right side cut short is marked *m*; *g*, round ligament, corresponding to gubernaculum; *i*, lower part of the intestine; *va*, vagina; *h*, situation of the hymen; C, gland of Bartholin (Cowper's gland), and immediately above it the urethra; *cc*, corpus cavernosum clitoridis; *sc*, vascular bulb or corpus spongiosum; *n*, nympha; *l*, labium; *v*, vulva.

Fallopian tubes, are formed out of the Müllerian ducts. That portion of the ducts in which they become fused together is developed into the vagina, the cervix, and part of the body of the uterus. The next following part of the Müllerian duct, constitutes in animals with horned uteri, the cornu of the uterus; but in the human subject it

Fig. 811.

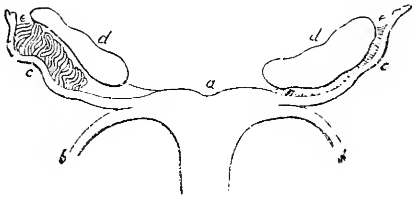


Fig. 811.—Female genital organs of the human embryo of three months with the remains of the Wolffian bodies (after J. Müller).

a, The body of the uterus notched above; *b*, the round ligament; *c*, the Fallopian tubes; *d*, the ovaries; *e*, remains of the Wolffian bodies.

remains comparatively short, entering into the formation of the upper part of the organ. The remaining upper portion of the Müllerian duct constitutes the Fallopian tube—becoming at first open and subsequently fringed at a short distance from its upper extremity.

Fig. 812.

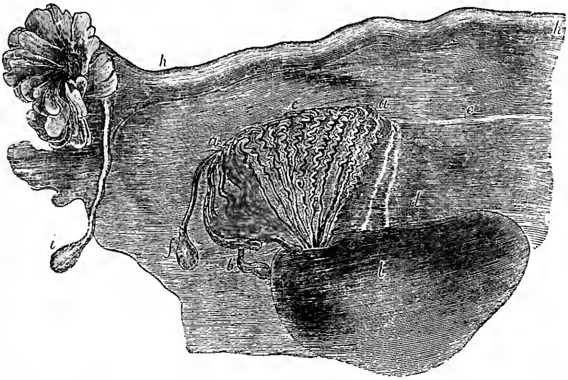


Fig. 812.—Adult ovary, parovarium and Fallopian tube (from Farre, after Kobelt).

a, *a*, Epoophoron (parovarium) formed from the upper part of the Wolffian body; *b*, remains of the uppermost tubes sometimes forming hydatids: *c*, middle set of tubes; *d*, some lower atrophied tubes; *e*, atrophied remains of the Wolffian duct; *f*, the terminal bulb or hydatid; *h*, the Fallopian tube, originally the duct of Müller; *i*, hydatid attached to the extremity; *l*, the ovary.

The additional or accessory fimbriæ and openings referred to by Henle in his Handbuch, vol. ii., p. 470, may admit of explanation on the supposition of the duct of Müller having remained open at these places.

In the human embryo of the third month the uterus is two-horned, and it is by a subsequent median fusion and consolidation that the triangular body of the entire organ is produced. The cornua uteri, therefore, of the human uterus cor-

respond with the separate cornua of the divided uterus in animals, and this explains the occasional malformation consisting in the greater or less division of the uterine cavity and vagina into two passages. There is no distinction in the human fœtus in the third and fourth month between the vagina and uterus. In the fifth and sixth months the os uteri begins to be formed, and the neck is subsequently gradually distinguished. Thickening succeeds in the walls of the uterine portion ; but this takes place first in the cervix, which up to the time of birth is much larger and thicker than the body of the uterus (Kölliker).

In the meantime the Wolffian bodies undergo a partial atrophy, and their ducts become more or less obliterated and abortive in different parts. The most constant vestige of the Wolffian bodies in the female is the now well-known body of Rosenmüller (No. 277) or Parovarium of Kobelt (No. 285) which has already been described at p. 720 of this volume, the *epoophoron* of Waldeyer, and which, being produced out of the same elements as the epididymis of the male, presents a remarkable resemblance to that body. The canal uniting the radiating tubes (coni vasculosi) of this organ is also usually persistent, but ceases at a short distance below. In the sow and several ruminants, however, and in some Simiæ, the subdivided upper tubular part or epoophoron has disappeared, and the main tube (middle part of the Wolffian duct) remains as the *duct of Gaertner*, a strong, slightly undulated tube, which is traceable, first free in the broad ligament of the uterus, and lower down becoming incorporated with the wall of the uterus and vagina, upon which last it is lost.

The Male Passages.—The conversion of the Wolffian duct into the vas deferens of the testicle was first demonstrated in animals by

Fig. 813.

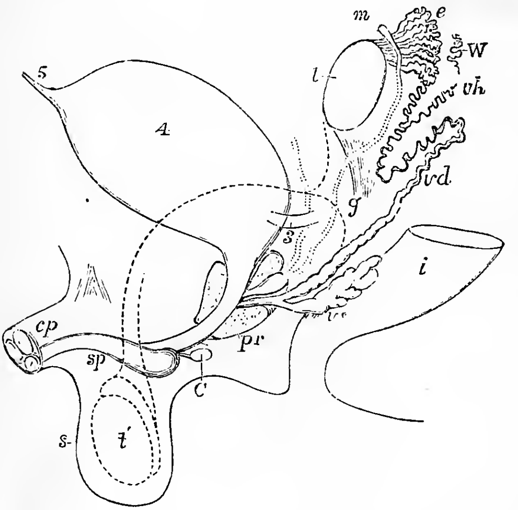


Fig. 813.—Diagram of the male type of sexual organs.

Compare with fig. 810 3, ureter ; 4, urinary bladder ; 5, urachus ; *t*, testicle in the place of its original formation ; *e*, caput epididymis ; *vd*, vas deferens ; W, scattered remains of the Wolffian body, constituting the organ of Giraldès, or the paradidymis of Waldeyer ; *v h*, vas aberrans ; *m*, Müllerian duct, the upper part of which remains as the hydatid of Morgagni, the lower part, represented by a dotted line descending to the prostatic vesicle, constitutes the occasionally existing cornu and tube of the uterus masculinus ; *g*, the gubernaculum ; *vs*, the vesicula seminalis ; *p r*, the prostate gland ; C, Cowper's gland of one side ; *c p*, corpora cavernosa penis cut short ; *s p*, corpus spongiosum urethræ ; *s*, scrotum ; *t′*, together with the dotted lines above, indicates the direction in which the testicle and epididymis change place in their descent from the abdomen into the scrotum.

Rathke (No. 278, Part 4), in correction of the views of J. Müller (No. 279), and was further proved and illustrated by H. Meckel (No. 284) and Bidder (No. 282). Kölliker showed that a similar process occurs in the human embryo, and that a communication established between the seminal tubes

of the testicle (rete testis) and some of the upper tubes of the Wolffian body gives rise to the epididymis.

In the male, the Müllerian ducts are destined to undergo little development and are of no physiological importance, while the ducts of the Wolffian bodies, and probably also some part of their glandular substance, form the principal part of the excretory apparatus of the testicle. The united portion of the Müllerian ducts remains as the vesicula prostatica, which accordingly not only corresponds with the uterus, as was shown by Weber (No. 283), but likewise, as pointed out by Leuckart (No. 288), contains as much of the vagina as is represented in the male. In some animals the vesicula prostatica is prolonged into cornua and tubes; but in the human subject the whole of the ununited parts of the Müllerian ducts disappear, excepting, as suggested by Kobelt, their upper extremities, which seem to be the source of the hydatid of Morgagni found between the body of the testicle and upper globe of the epididymis. The excretory duct of the Wolffian body, from the base of that body to its orifice, is converted into vas deferens and ejaculatory duct, the vesicula seminalis being formed as a diverticulum from its lower part (Waldeyer).

With respect to the formation of the epididymis, it appears certain that the larger convoluted seminal tube, which forms the main part and globus minor of that body, arises by a change or adaptation of that part of the Wolffian duct which runs along the outer side of the organ. The vas aberrans or vasa aberrantia of Haller appear to be the remains also, in a more highly convoluted form, of one or more of the tubes of the Wolffian body still adhering to the excretory duct of the organ, and their communication with the main tube of the epididymis receives an explanation from that circumstance. As to the coni vasculosi in the upper part of the epididymis, it has been customary to regard them as produced by a transformation of some of the tubes in the upper part of the Wolffian body, according to the views most fully given by Kobelt; but, from more recent observations, Banks has described the origin of the coni vasculosi as more probably due to a process of development occurring in a new structure or mass of blastema which had been previously observed by Cleland, and which is formed in connection with the upper part of the Wolffian body, and close to the Müllerian duct; while Kölliker holds that sufficient evidence has not yet been adduced in favour of this view.

The coni vasculosi, becoming convoluted, are connected with the body of the testicle by means of a short straight cord, which is afterwards subdivided into the vasa efferentia. The peritoneal elevation descending from the testis towards the

Fig. 814.

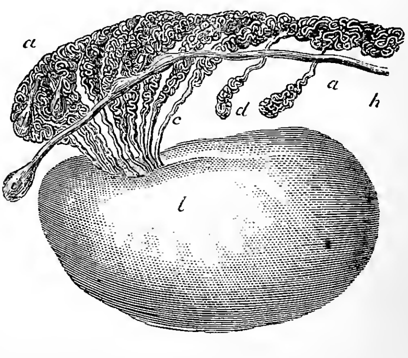


Fig. 814.—View from before of the adult testis and epididymis (from Farre, after Kobelt).

a, a, convoluted tubes in the head of the epididymis developed from the upper part of the Wolffian body; *b* and *f*, hydatids in the head of the epididymis; *c*, coni vasculosi; *d*, vasa aberrantia; *h*, remains of the duct of Müller with *i*, the hydatid of Morgagni at its upper end; *l*, body of the testis.

lower extremity of the Wolffian body, is the upper part of the plica gubernatrix, and becomes shortened as the testicle descends to meet the lower end of the epididymis; the peritoneal elevation which passes down into the scrotum, and is continuous with the first, is the more important part of the plica gubernatrix, connected with the gubernaculum testis. The spermatic artery is originally a branch of one of those which go to the Wolffian body, and

ascend from the surface of the Wolffian body to the upper part of the testis, along the ligaments connecting them; but, as the testis descends, the artery lies entirely above it, the secreting substance of the Wolffian body remaining adherent to it; and hence it is that the organ of Giraldès, which consists of persistent Wolffian tubules, is found in a position superior to the epididymis. (Banks, No. 290).

The Descent of the Testicles.—The testicles, which are originally situated in the abdominal cavity, pass down into the scrotum before birth. The testicle enters the internal inguinal ring in the seventh month of fœtal life: by the end of the eighth month it has usually descended into the scrotum, and, a short time before birth, the narrow neck of the peritoneal pouch, by which it previously communicated with the general peritoneal cavity, generally becomes closed, and the process of peritoneum, now entirely shut off from the abdominal cavity, remains as a separate serous sac. The peritoneal pouch, or processus vaginalis, which passes down into the scrotum, precedes the testis by some time in its descent, and into its posterior part there projects a considerable columnar elevation. There is likewise a fibrous structure attached inferiorly to the lower part of the scrotum, and surrounding the peritoneal pouch above, which may be distinguished as the *gubernacular cord*, both this and the plica gubernatrix being included in the general term *gubernaculum testis* (J. Hunter, No. 276). The gubernacular cord consists of fibres which pass downwards from the sub-peritoneal fascia, others which pass upwards from the superficial fascia and integument, and others again which pass both upwards and downwards from the internal oblique muscle and the aponeurosis of the external oblique; it exhibits, therefore, a fusion of the layers of the abdominal wall. Superiorly, it surrounds the processus vaginalis, without penetrating the plica gubernatrix; and the processus vaginalis, as it grows, pushes its way down through the gubernacular cord and disperses its fibres. By the time that the testis enters the internal abdominal ring, the processus vaginalis has reached a considerable way into the scrotum; and, as the testis follows, the plica gubernatrix becomes shorter, till it at last disappears; but it cannot be said that the shortening of the plica is the cause of the descent of the testicle, and much less that (as has been held by some) the muscular fibres of the gubernacular cord are the agents which effect this change of position. The arched fibres of the cremaster muscle make their appearance on the surface of the processus vaginalis as it descends, while its other fibres are those which descend in the gubernacular cord. (See Cleland, No. 289).

3. **The External Organs.**—In the human embryo, as before stated with respect to animals, the external organs are up to a certain time entirely of the same form in both sexes; and the several organs which afterwards distinguish the male and female externally take their origin respectively from common masses of blastema of precisely similar structure and connections. The common cloaca exists till after the fifth week, and the genital eminence from which the clitoris or penis is formed makes its appearance in the course of the fifth and sixth weeks in front of and within the common orifice. In the course of the seventh and eighth weeks the common orifice is seen to become divided into two parts, viz., the longer slit of the genito-urinary aperture anteriorly, and the narrower and more rounded anal aperture posteriorly: but the exact manner in which the separation of these two apertures takes place has not yet been accurately traced. This process is intimately connected with the formation of the urogenital cord as an independent structure, and is probably mainly effected by the advance from the sides and posteriorly of septal bands which divide the cloaca into a dorsal or anal and a ventral or urogenital part. Somewhat later, or in the ninth and tenth weeks, a transverse integumental band completes the division between the anal and the urogenital orifices, which band forms the whole of the

so-called perineum of the female, and the part of the perineal integument in the male which is situated behind the scrotum; the raphé being most obvious in the male sex.

Two apertures are now seen to occupy the perineal region. Of these the dorsal one or anus is of a rounded form and small size, and is surrounded by a small circular integumental ridge; the anterior or urogenital aperture forms a narrow vertical slit wider behind than before, and running forward into the rudiment of the penis, or clitoris.

The well marked eminence in the integument which forms this rudiment, at first indifferent in the two sexes, is surrounded by a deep circular fold of the integument which encompasses its base, and which in the separate condition is the foundation of the mons veneris and labia majora in the female, and when

Fig. 815.

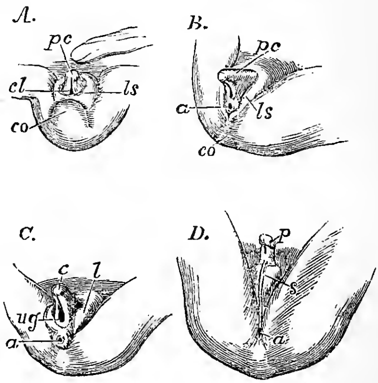


Fig. 815.—Development of the external sexual organs in the male and female from the indifferent type (from Ecker).

A, the external sexual organs in an embryo of about nine weeks, in which external sexual distinction is not yet established, and the cloaca still exists; B, the same in an embryo somewhat more advanced, and in which, without marked sexual distinction, the anus is now separated from the uro-genital aperture; C, the same in an embryo of about ten weeks, showing the female type; D, the same in a male embryo somewhat more advanced. Throughout the figures the following indications are employed; *pc*, common blastema of penis or clitoris; to the right of these letters in A, the umbilical cord; *p*, penis; *c*, clitoris; *cl*, cloaca; *ug*, urogenital opening; *a*, anus; *ls*, cutaneous elevation which becomes labium or scrotum; *l*, labium; *s*, scrotum; *co*, caudal or coccygeal elevation.

united by median fusion, of the scrotum in the male. The lips of the urogenital furrow, which in the female are converted into the nymphæ, and in the male unite as integument below the penis, are both at first precisely the same in all embryoes. In the open condition, which continues until the eleventh or twelfth week, the parts appear alike in both sexes, and resemble very much the more advanced female organs. The rudiments of *Bartholin's* or *Cowper's glands* are. it is said, seen at an early period, near the root of the rudimentary clitoris or penis, on each side of the genito-urinary passage.

In the female, the two external folds of integument enlarge, so as to cover the clitoris as the *labia majora*. The clitoris itself remains relatively smaller, and the groove on its under surface becomes less and less marked, owing to the opening out, and subsequent extension backwards, of its margins to form the *nymphæ*. The vascular bulbs, sunk more deeply in the tissues, remain distinct and separate, except at one point where they run together in the glans clitoridis. The *hymen* begins to appear about the fifth month as a fold of the lining membrane at the opening of the genital passage into the urogenital sinus. Within the vestibule, which is the shortened but widened remains of the urogenital sinus, the urethral orifice is seen, the urethra itself undergoing considerable elongation.

In the male, on the contrary, the *penis* continues to enlarge, and the margins of the groove along its under surface gradually unite from the primitive urethral orifice behind, as far forwards as the glans, so as to complete the long canal of the male *urethra*, which is therefore a prolongation of the urogenital sinus. This

is accomplished about the fifteenth week. When this union remains incomplete, the abnormal condition named *hypospadias* is produced. In the meantime the *prepuce* is formed, and, moreover, the lateral cutaneous folds also unite from behind forwards, along the middle line or *raphé*, and thus complete the *scrotum*, into which the testicles descend in the course of the eighth month of fœtal life, as before described.

The corpora cavernosa, which are at first separate, become united in their distal portions in both sexes; but the corpus spongiosum urethræ which is also originally divided in all embryoes, and in the female remains so in the greater part of its extent, becomes enlarged in the male in the glans penis, and its two parts united mesially both above and below the urethra, so as to enclose the whole of that tube from the bulb forwards to the glans.

TYPE OF DEVELOPMENT AND ABNORMAL FORMS.

The type of development in the several parts of the genital organs may be stated to differ in the two sexes as follows, viz. :—

1st. In the external organs it is single and homological. 2nd. In the middle organs or passages it is double and heterological. 3rd. In the productive organs it is single and homological as regards the productive elements, but with some difference of the sources from which the containing capsules of the ovary or tubes of the testicle are respectively derived. This is illustrated by the table placed on p. 911.

Accordingly the congenital malformations of the reproductive organs admit of being distributed under the following divisions :—

1st. Abnormal forms attributable to variations in the development of one or more of the external organs in either sex, producing an approach to the form of the other sex.

2nd. Forms referrible to variations in the development of the Wolffian or Müllerian ducts, so as to lead to the greater or less predominance of sexual characters in a part or the whole of either of these passages inconsistent with those prevailing in other parts of the system, or to the coexistence of both sets of passages in whole or in part.

3rd. Extremely rare forms referrible to the possible coexistence of the productive parts of testicles and ovaries in the same individual, which may be combined with more or less of the foregoing kinds of malformation.

As an example of this last form reference may be made to the case described by Heppner, of St. Petersburg, in which microscopic examination showed the presence of small ova in Graafian follicles in the one pair of bodies and of seminiferous tubes and spermatic cells in the other. (No. 334.)

Upon the subject of Hermaphroditism consult Simpson (No. 333).

MALFORMATIONS IN GENERAL.

In the preceding pages we have frequently had occasion to refer to the relation subsisting between the natural development of organs and their abnormal conditions or malformations. There can be no doubt that a considerable number of congenital malformations, more especially those of the nature of *defect*, whether by non-formation or deficient growth of the parts in which they occur, or by want of union between those which naturally fuse together, as well as many abnormal conditions depending on misplacement and altered form and structure, may be attributed in some measure to an arrest of the process of development, or a variation in some part of it, in the earlier stages of embryonic life, and may therefore receive much illustration from the study of the natural process of formation. But comparatively little light has yet been thrown by this study upon the origin of that large class of malformations in which there is *redundance* of parts, either by more or less complete duplicity of the whole body, or by an increase in the number of individual parts. At the same time it is obvious that, since in these as in all other malformations the histological and morphological processes of development do not differ essentially in their nature from the natural ones, but are only modifications and variations of them, the

knowledge of the true nature of the abnormal structures must follow closely upon our acquaintance with the natural processes of development.

Upon this extensive subject, which does not come within the scope of this work, the reader is referred to the masterly Essay of Bischoff (No. 312), and other treatises quoted in the Bibliography at p. 918.

Tabular scheme of the CORRESPONDING PARTS of the genito-urinary organs in the two sexes, and of their relation to their EMBRYONAL ELEMENTS :—

I.—GERMINAL RIDGE.

ADULT FEMALE.	EMBRYONAL.	ADULT MALE.
Ova.	1. Germ-epithelium	**Spermatic cells.**
Stroma of the ovary and Graafian follicles.	2. Deeper blastema with Wolffian stroma.	**Seminal tubes.**

II.—MULLERIAN DUCTS.

(Ducts of Pronephros.)

ADULT FEMALE.	EMBRYONAL.	ADULT MALE.
Fimbriated Fallopian opening and occasional hydatids.	1. Anterior extremity	**Hydatid of Morgagni.**
Fallopian tubes	2. Middle part........................	Tubes extending from the uterus masculinus.
Vagina and uterus	3. Posterior single part	**Uterus masculinus or prostatic vesicle.**

III.—WOLFFIAN BODIES (MESONEPHROS).

ADULT FEMALE.	EMBRYONAL.	ADULT MALE.
Smaller tubes of **epoophoron**, Organ of Rosenmüller (Parovarium.)	1. Anterior segmental tubes.	**Vasa efferentia** and coni vasculosi of the epididymis.
Paroophoron (Wald.)	2. Posterior segmental tubes...	**Paradidymis** (Wald.), organ of Giraldès, and vasa aberrantia.
Round ligament of the uterus....	3. Ligament of the Wolffian body.	**Gubernaculum testis.**

IV.—WOLFFIAN DUCTS.

ADULT FEMALE.	EMBRYONAL.	ADULT MALE.
Main Tube of the Epoophoron ...	1. Anterior and middle parts...	Convoluted tube of the **epididymis.**
Ducts of Gaertner, of some animals.	2. Posterior part........................	**Vas deferens** and vesiculæ seminales.

V.—METANEPHROS.

ADULT FEMALE.	EMBRYONAL.	ADULT MALE.
Kidney	1. Tubular portion	**Kidney.**
Ureter	2. Duct	**Ureter.**

VI.—GENITAL CORD AND SINUS UROGENITALIS.

ADULT FEMALE.	EMBRYONAL.	ADULT MALE.
Tissue uniting female urethra and vagina.	1. Substance surrounding genital cord.	**Prostate gland.**
Female urethra	2. Urinary pedicle.	**Prostatic portion of urethra** above **vasa deferentia.**
Ostium vaginæ. Hymen	3. Confluence of genital with urinary parts.	**Verumontanum.**
Vestibule	4. Lower part	Lower **prostatic** and **membranous part of urethra.**
Bartholin's Glands	5. Common blastema	**Cowper's Glands.**

VII.—EXTERNAL ORGANS.

1.—*Vascular parts.*

ADULT FEMALE.	EMBRYONAL.	ADULT MALE.
Crura and corpus clitoridis	*a.* Corpora cavernosa	Crura and **corpus penis.**
Glans clitoridis and vascular bulbs	*b.* Corpora spongiosa	**Glans penis** and **spongy body.**

2.—*Integumental parts.*

ADULT FEMALE.	EMBRYONAL.	ADULT MALE.
Preputium clitoridis	*a.* On genital eminence	**Preputium penis.**
Folds of **nymphæ**	*b.* Lips of genital ridges	**Raphé** below penis.
Mons veneris and **labia majora** ...	*c.* Cutaneous wall	**Pubic eminence** and **scrotum.**
Perineum of female, with raphé...	*d.* Transverse ano-genital band	**Perineum** of male behind scrotum, with raphé.

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